GROWTH, FORAGING BEHAVIOR AND DISTRIBUTION OF AGE-0 ARCTIC GRAYLING IN AN ALASKAN STREAM

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GROWTH, FORAGING BEHAVIOR AND DISTRIBUTION OF AGE-0 ARCTIC GRAYLING IN AN ALASKAN STREAM

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Abstract

I evaluated the ability of three models to relate habitat characteristics to habitat quality for age-0 Arctic grayling *Thymallus arcticus* in an Alaskan stream. A temperature-based growth model made accurate predictions, showing it can reliably assess thermal habitat quality. Deviations between predicted and observed growth were useful because they identified the timing of possible critical periods, when competition for food or space may cause density-dependent mortality and emigration. A foraging model consistently overestimated the mean prey size of fish, showing that such models need further work before they can accurately assess food availability from invertebrate drift. A habitat selection model accurately predicted small fish would occupy the stream margins and the ontogenetic shift into faster, deeper water, but its detailed predictions for larger fish were not very precise. These models were useful tools for assessing habitat quality and gave insight into possible interactions between habitat characteristics and population dynamics.

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INTRODUCTION

Natural and human perturbations can alter the physical, chemical and biological attributes of streams and change their productive capacity for fish (Sempeski and Gaudin 1995; Reeves et al. 1998). It is crucial to successful mitigation and management efforts to be able to predict consequences of these alterations for fish and identify habitat conditions or management efforts that favor fish growth and survival. Relating differences in growth and survival to differences in habitat conditions also provides an opportunity to test ecological theory and to apply basic ecological understanding to management or conservation (Nislow 1997).

Growth, foraging and habitat selection models are among the most promising tools available for predicting how habitat characteristics translate into habitat quality, and for predicting the consequences of habitat change. In this study, I tested the ability of these models to evaluate different aspects of habitat quality for age-0 Arctic grayling *Thymallus arcticus* in Chena Slough. My goal was to determine whether the models were capable of explaining why Chena Slough is currently such a highly productive nursery and rearing area for Arctic grayling and to determine whether these models might be useful for predicting the effects of the habitat changes that are occurring in the Slough, or provide insight into habitat restoration and enhancements efforts.

I chose to study Chena Slough because this small groundwater-fed stream has become one of the most important spawning and rearing areas for Arctic grayling in the Chena River drainage (Tack 1976; Walker 1983). The Chena River historically supported the largest Arctic grayling sport fish harvest in North America, and is now a

world-class catch-and-release sport fishery (Ridder and Fleming 1997). Chena Slough is also undergoing rapid habitat change, a consequence of both urbanization of the watershed and natural succession. There is considerable interest among fisheries managers and the public as to whether these changes are positive or negative for Arctic grayling (Tack 1971; Wuttig 1997), but there is little scientific evidence to address these issues.

The three models I tested are designed to evaluate different aspects of habitat quality. In Chapter One, I assess the ability of a temperature-based growth model (Mallet et al. 1999) to predict length-at-age for age-0 Arctic grayling and evaluate thermal habitat quality. Predicting the seasonal growth of fish from a description of the seasonal temperature regime can be used to assess the quality of fish habitat, provide insight into plausible mechanisms regulating growth, and enable biologists to detect periods when growth is restricted or changes in growth. I analyzed the relationship between predicted growth and observed growth for any indication of competition due to resource limitation during the first growing season. In particular I was interested to see if it might be possible to identify the timing of possible bottlenecks or critical periods during which density-dependent mortality might be operating to establish year-class strength.

In Chapter Two, I test the ability of a foraging model developed by Hughes and Dill (1990) and Hughes (1998) to accurately predict the size composition of the diet of age-0 Arctic grayling. An ecological analysis of the diet can indicate the relative importance of actual prey eaten and provide insight on the type of food available in the

stream environment (Wootton 1990). Understanding the diet of juvenile Arctic grayling and its influence on growth can be essential to understanding the ecological function and productive capacity of the population in Chena Slough. I was interested in establishing whether the model could be used to estimate the profitability of foraging habitat for juvenile rearing.

In Chapter Three, I assess the ability of a habitat selection model (Hughes and Dill 1990 and Hughes 1998) to predict the distribution patterns of age-0 Arctic grayling within a reach and the ontogenetic habitat shift into faster, deeper water. Habitat where the net rate of energy intake is greatest represents physical habitat conducive to high fish growth. I selected this model because I wanted to establish whether the model could be used to determine rearing habitat quality and differences in rearing quality between two reaches. I was interested in knowing if model predictions could be combined with the logic of Ideal Free Distribution theory (Fretwell and Lucas 1970) to explain changes in relative fish abundance between the two reaches.

In the final chapter, I summarize the results of the three models, provide general conclusions for the study, and make recommendations for future research.

STUDY SITE

I collected data from Chena Slough in interior Alaska (Figure 1). Chena Slough was one of several side channels of the Tanana River that carried large volumes of glacial water to the Chena River (Collins 1990). In 1941, flood control activities blocked the upper end of Chena Slough creating a clear-flowing stream fed by

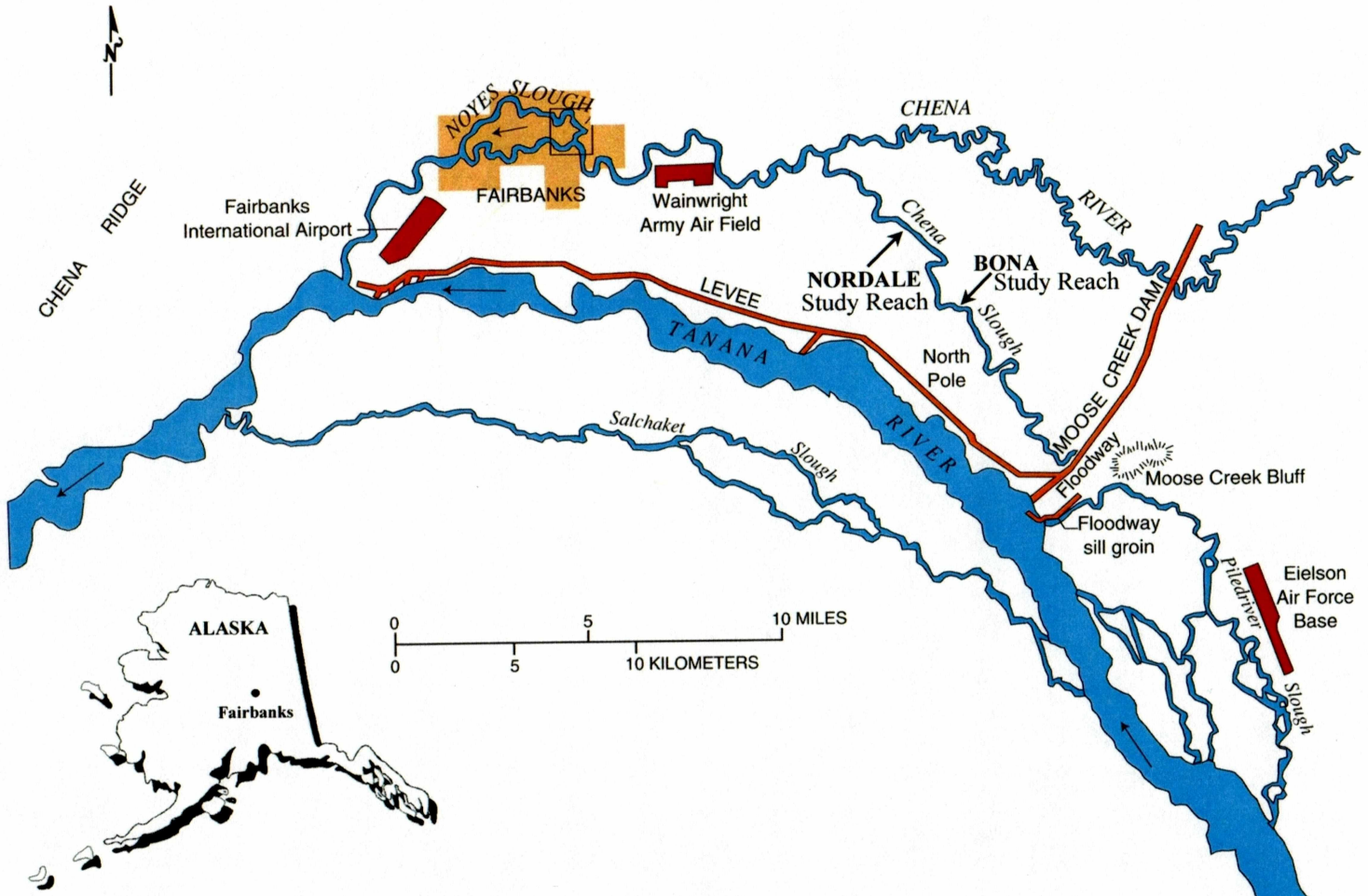

Figure 1.-Map of Chena Slough showing present-day flood control structures and study reaches (Nordale and Bona). Modified from Burrows et al. (2000).

upwelling groundwater from the Tanana Aquifer (Nelson 1978; Krumhardt 1982). Currently, Chena Slough (known locally as Badger Slough) is a small, low-gradient stream 15-30 m wide and 27 km in length, with a summer discharge averaging about 1.2 m^3/s (R. Burrows, USGS, personal communication). Annual water temperatures generally range from 1 to 19 °C, with summer temperatures averaging 2-4 °C warmer than the main stem Chena River (Walker 1983). The streambed consists primarily of gravel overlaid in many areas with a thick layer of organic mud that supports a dense growth of aquatic macrophytes (*Hippuris vulgaris*, *Potomageton alpinus*, *Sparganium* sp., and *Ranunculus aquatilis*) and algae (diatoms, *Nostoc* sp. and filamentous algae). The combination of constant flow, warm water temperatures, shallow gravel riffles, and high productivity have created favorable spawning and rearing habitat for Arctic grayling (Ridder and Fleming 1997).

Since 1941, urban runoff and septic leakage from development along Chena Slough has caused cultural eutrophication, consequently, the growth of aquatic vegetation and its decomposition have resulted in suspended debris and thick deposits of organic mud. This, together with encroachment of emergent and terrestrial vegetation is thought to have reduced the quantity and quality of available spawning and rearing habitat and, possibly, the productive capacity for juvenile Arctic grayling (Tack 1971; Wuttig 1997).

Study Reaches

I sampled two reaches in Chena Slough; both are riffle sections located within the mid-section of the Slough where the highest densities of age-0 Arctic grayling are found.The Nordale reach is downstream of the Nordale Road crossing and approximately 7.5 km upstream of the confluence of the Chena River (Figure 2). It is 20 m in length and up to 20 m in width. There are two large culverts just above the study site, with one beaver dam located approximately 50 m upstream of this crossing and another approximately 300 m downstream. The streambed consists primarily of small gravel and a few large boulders. Some areas are covered with thick emergent vegetation and the north stream margins consist of several large woody debris. The Bona reach is approximately 6 km upstream of Nordale between Plack and Repp Road crossings (Figure 3). It is 20 m in length and up to 12 m in width. There are no road culverts or other flow diversions within 1 km of the site. Extensive, thick overflow ice or *aufeis* can be seen along the south bank through early to mid June. The streambed consists primarily of cobble covered with high concentrations of benthic algae.

Figure 2.-Aerial view of the Nordale study reach.

Figure 3.-Aerial view of the Bona study reach.

CHAPTER 1: Assessing the Ability of a Temperature-Based Growth Model to Predict Growth of Age-0 Arctic Grayling and Identify Critical Periods

Abstract

I tested the ability of a temperature-based growth model for European grayling *Thymallus thymallus* (Mallet et al. 1999. Can. J. Fish. Aquat. Sci. 56:994-1000) to predict the growth rate of age-0 Arctic grayling *T. arcticus*. I examined observed and predicted growth curves, and analyzed changes in the length-frequency distribution for periods of competition due to food limitation. The model accurately predicted growth in one reach, but in the other, observed growth fell below predicted growth. This departure occurred when fish were 4-5 weeks old, corresponding with an increase in the coefficient of variation and in the positive skewness of the length-frequency distribution. Results showed that the model could be used to predict growth rates and determine thermal habitat quality for Arctic grayling. The model was also able to identify possible critical periods caused by intense food competition, where density-dependent mortality or emigration can act to establish year-class strength.

Introduction

Bioenergetic models that predict fish growth from habitat characteristics have become an important tool for predicting fish growth and assessing habitat quality (Kitchell et al. 1977; Edwards et al. 1979; Elliott 1984b, 1989b, 1994; Preall and Ringler 1989; Brant et al. 1992; Rand et al. 1993; Lobón-Cerviá and Rincón 1998; Hughes 1998; Mallet et al.1999). Typically these models predict fish growth using information on water temperature and daily ration of the fish. However, Elliott (1984b; 1988; 1989a; 1990; 1994) has shown that temperature alone can accurately predict growth of age-0 brown trout *Salmo trutta* in the field, and that mean growth rates are unrelated to fish density. This finding is important because it shows that mean growth rates may not be sensitive to the intensity of competition when we might expect daily ration to be reduced. Elliott also found that competition for territories shortly after fry emergence resulted in a critical period during which size-selective density-dependent mortality and emigration reduced the coefficient of variation (CV) in fish length (Elliott 1984a, 1984b, 1987; 1988; 1989a, 1989b, 1989c; 1990; 1994).

In contrast to Elliott's findings, other studies suggest that it is not possible to predict growth rates of age-0 salmonids from temperature alone because growth rates decrease as fish density increases and per-capita resource availability declines (Jenkins et al. 1999; Keeley 2001). Keeley's study of steelhead trout *Oncorhynchus mykiss* provides an interesting contrast to Elliott's results; as per-capita resource abundance fell, growth rates were reduced, CV in fish length increased, and the length-frequency distribution developed an increasingly positive skew. Under these circumstances it

would not be possible to use temperature alone as a measure of thermal habitat quality without including ration size.

The purpose of this study was to assess whether a temperature-based growth model developed by Mallet et al. (1999) for European grayling *Thymallus thymallus* could be used to evaluate thermal habitat quality.

My first objective was to test whether the model could accurately predict the growth rate of age-0 Arctic grayling *T. arcticus* in the field.

My second objective was to determine whether a comparison of predicted and observed growth rates could provide insight into the timing of critical periods during which density-dependent mortality might be operating to establish year-class strength. For example, if Arctic grayling are similar to steelhead trout (Keeley 2001), we would expect observed growth to fall below predicted growth during periods of intense competition, and we would expect to see an increase in CV in length and an increase in positive skewness of length-frequency distributions. On the other hand, if Arctic grayling are similar to brown trout (Elliott 1984a, 1984b, 1987; 1988; 1989a, 1989b, 1989c; 1990; 1994), we would not expect observed growth to fall below predicted growth during periods of intense competition, but we would expect to see a reduction in the CV in length. This comparison may demonstrate that growth models can be beneficial in examining population dynamics of age-0 Arctic grayling.

Growth Model

The growth model developed by Mallet et al. (1999) for European grayling describes the rate of change in length (L_t) with time (t). The model can be used to calculate the daily growth increment (L_{t+1}) of the fish as follows:

(1) $$L_{t+1} = \bar{k}(L_\infty - L_t)$$

where $\bar{k} = k_{opt} X_T$

and $$X_T = \frac{(T - T_{\min})(T - T_{\max})}{(T - T_{\min})(T - T_{\max}) - (T - T_{opt})^2}$$

where $\bar{k}$ is the temperature sensitive growth coefficient, L_∞ is the asymptotic length, L_t is length at age t, k_{opt} is the growth coefficient at the optimum temperature for growth, X_T is the coefficient of temperature, T is the mean daily water temperature (°C), T_{min} is the minimum temperature at which growth occurs, T_{max} is the maximum temperature at which growth occurs, and T_{opt} is the temperature at which growth is maximum. Figure 4. illustrates the relationship between the growth coefficient (k) and daily water temperature (T) for European grayling.

Parameter estimates for the model are given in Table 1. I used parameter values established for European grayling in the model because (1) maximum, optimum and minimum temperatures for growth have not been established for Arctic grayling; (2) the value for the growth coefficient at optimum temperature for growth (k_{opt}) has not been

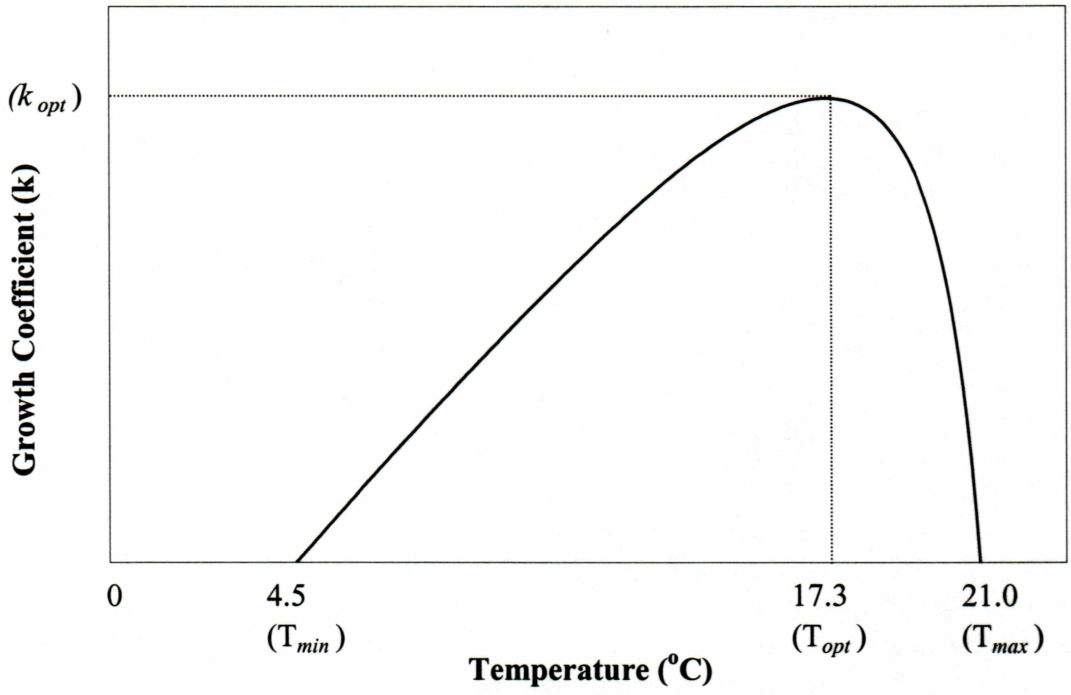

Figure 4.-Relationship between the growth coefficient (k) and mean daily water temperature (T). Modified from Mallet et al. (1999).

Table 1.-Parameter estimates for the growth model from Mallet et al. (1999).

Parameter	Value
L_{∞} (mm)	450
k_{opt}	0.002699
T_{min} (°C)	4.5
T_{opt} (°C)	17.3
T_{max} (°C)	21.0

established for Arctic grayling; and (3) the asymptotic length for European grayling was close to maximum lengths of Arctic grayling in interior Alaska (Armstrong 1986).

Methods

Data Collection

I collected data on temperature and fish length from the two reaches to test the growth model. I recorded daily water temperatures (°C) to describe the seasonal temperature regime. I deployed temperature data loggers at the nearest road crossings (Nordale Road; and Repp and Plack roads) from 25 May to 30 September in 2000 and within each study reach from 18 May to 3 October in 2001. Water temperatures were recorded hourly and daily means were calculated by averaging hourly temperatures.

I measured fork length (mm) of fish weekly at both study reaches, from shortly after they emerged from the gravel, starting 5 June in 2000 and 31 May in 2001, until the end of September to determine the growth rates of Arctic grayling and characterize length-frequency distributions. A weekly sub-sample of 25 fish were sampled in 2000, all fish seined were sampled each week in 2001. Larval fish were collected using hand-held aquarium nets, and 3 mm mesh seines were used for larger fish. I anesthetized fish with clove oil (0.1 ml clove oil to 100 ml water) to facilitate accurate measurement.

Analysis

I calculated and plotted model growth curves (average predicted weekly lengths from daily growth increments) along with average weekly-observed lengths for

comparison. I assessed model accuracy by calculating the sum of the unexplained residual variations, or squared normalized residuals (SNR) between observed and predicted lengths for each reach.

$$SNR = \frac{1}{n}\sum_{i=1}^{n}\frac{(\bar{L}_{predicted_i} - \bar{L}_{observed_i})^2}{\bar{L}_{predicted_i}} \quad (2)$$

where n is the number of weekly average lengths observed for each data set and i is a subscript designating the week.

I examined the predicted and observed growth curves for episodes where the observed growth curve fell below the predicted growth curve to evaluate evidence for competition. I also calculated the coefficient of variation (CV) in length and the skewness of the length-frequency distributions for each week. This enabled me to determine whether there was any evidence of density-dependent mortality.

Results

Predicted vs. Observed Growth Rates

Model results and seasonal temperature regimes for Nordale are shown in Figures 5 (2000) and 6 (2001). There was close agreement between observed and predicted growth curves at Nordale in both years (SNR = 0.156 in 2001 and SNR = 0.168 in 2000). The model accurately accounted for the difference in between-year growth rates and was able to closely match maximum fish length at the end of the

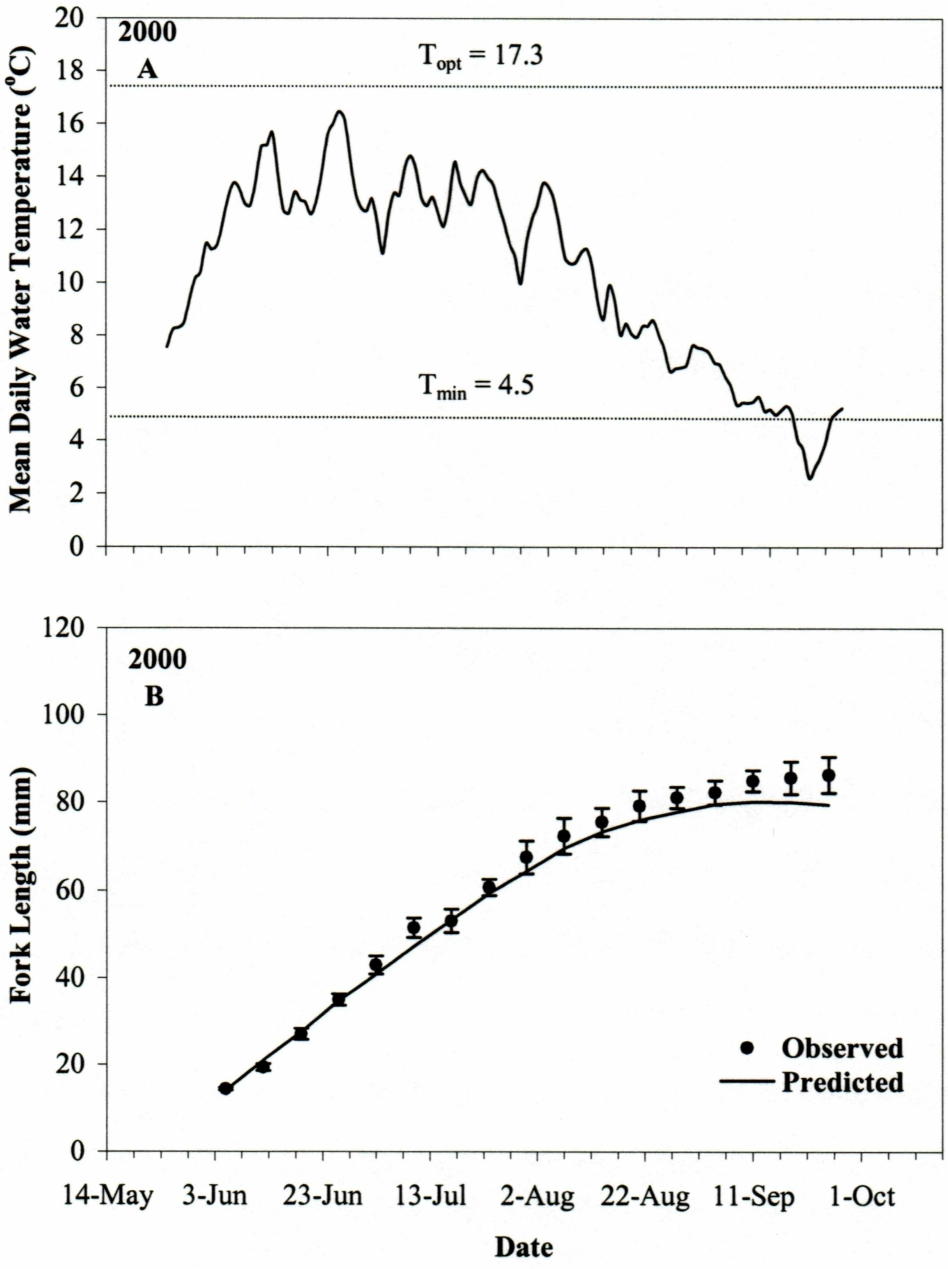

Figure 5.-Mean daily water temperatures (A), and predicted and observed lengths (B) with 95% confidence intervals for Nordale, 2000. Minimum temperatures (T_{min}) and optimum temperatures (T_{opt}) for age-0 Arctic grayling.

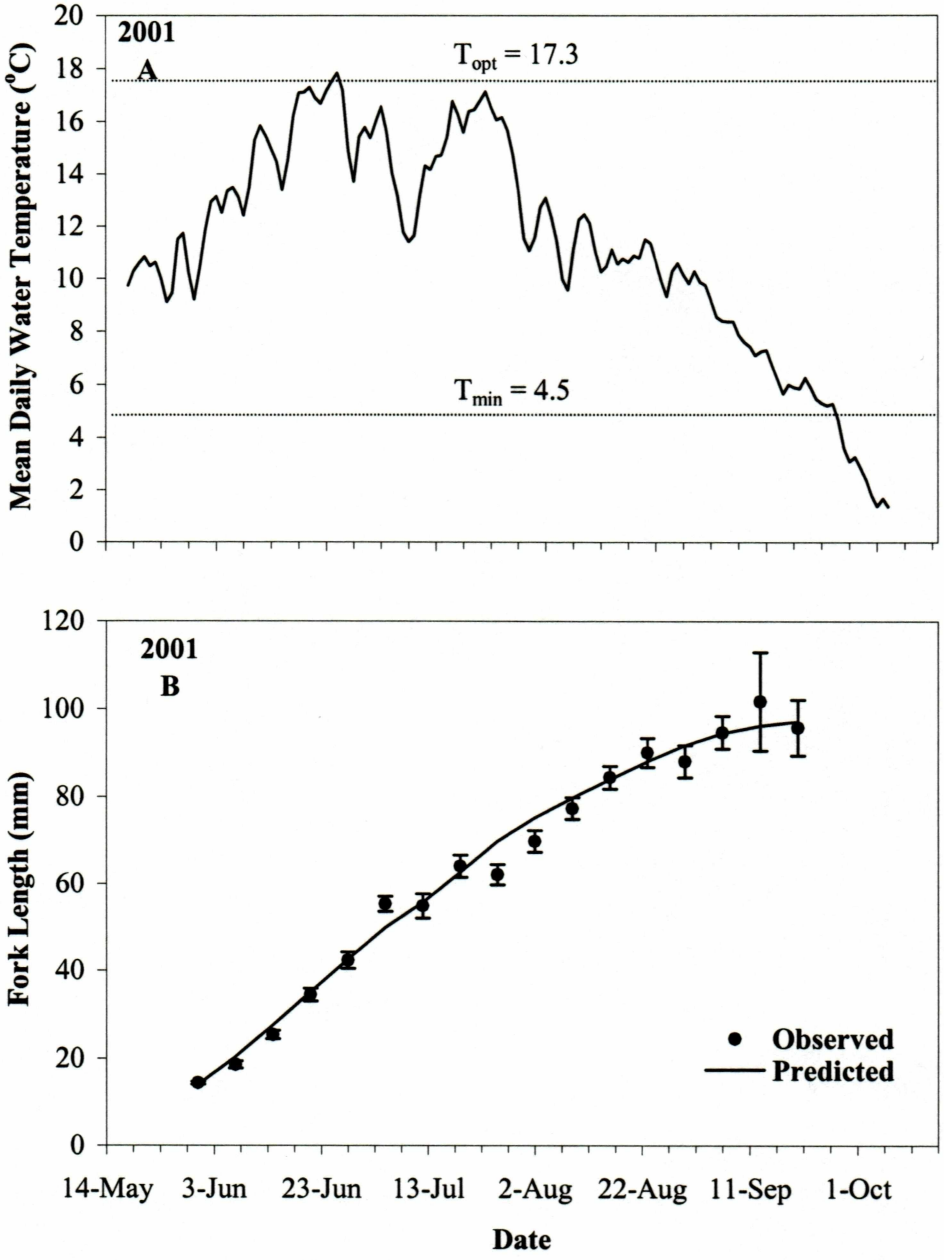

Figure 6.-Mean daily water temperatures (A), and predicted and observed lengths (B) with 95% confidence intervals for Nordale, 2001. Minimum temperatures (T_{min}) and optimum temperatures (T_{opt}) for age-0 Arctic grayling.

growing season (observed = 79, predicted = 86 in 2000; observed = 96, predicted = 97 in 2001).

Model results and seasonal temperature regimes for Bona are shown in Figures 7 (2000) and 8 (2001). The overall fit was not as good as Nordale (SNR = 2.399 in 2000 and SNR = 2.023 in 2001). In both years observed growth dropped below predicted growth when the fish were 4-5 weeks old. This departure was characterized by a cessation in observed growth for a two-week period. In 2000, observed growth remained well below the predicted curve (observed = 66, predicted = 83 on 11 September) and in 2001, observed growth rebounded to just below predicted (observed = 89, predicted = 93 on 13 September).

Evidence for Density Dependent Growth

Comparison of the growth curves shows that observed growth was much lower than predicted growth at Bona for a 2-week period beginning when Arctic grayling were 4-5 weeks old. Examination of the length-frequency histograms for Bona (Figures 9 and 10) show that these episodes of low growth corresponded with an increase in the CV in length and an increase in positive skewness for both years (Figure 11). This pattern was not evident at Nordale during either year (Figures 12, 13, and 11).

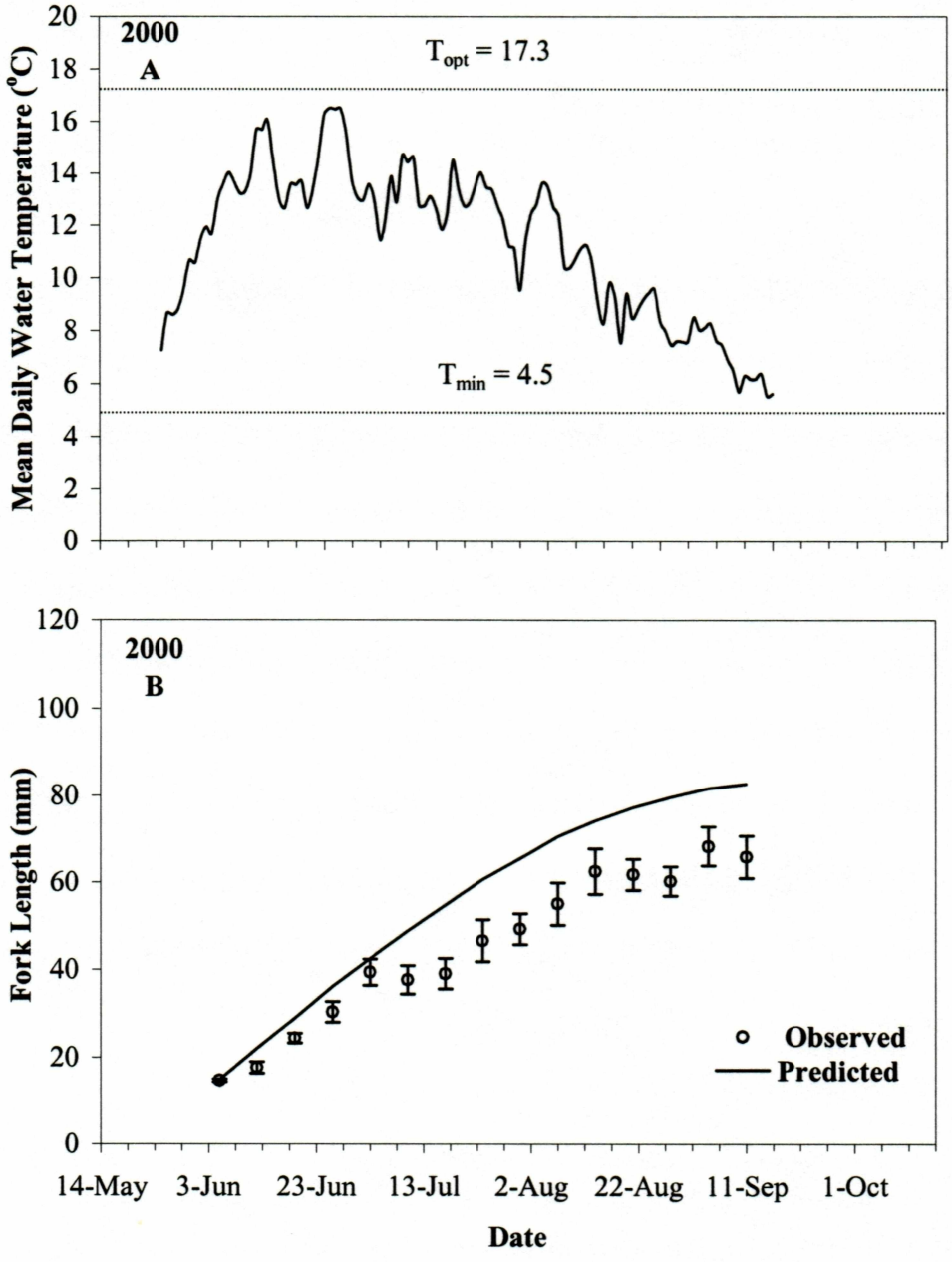

Figure 7.-Mean daily water temperatures (A), and predicted and observed lengths (B) with 95% confidence intervals for Bona, 2000. Minimum temperatures (T_{min}) and optimum temperatures (T_{opt}) for age-0 Arctic grayling.

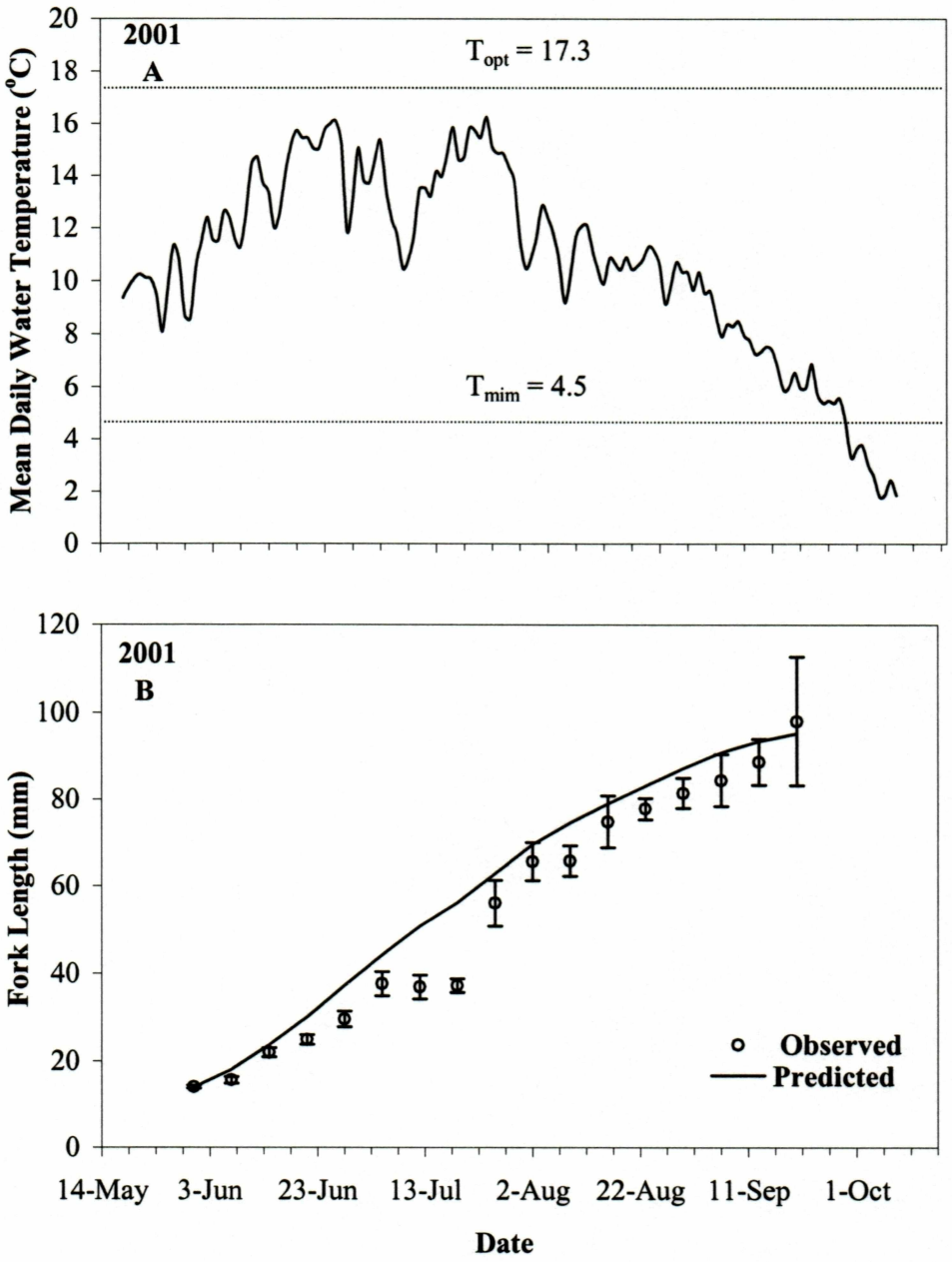

Figure 8.-Mean daily water temperatures (A), and predicted and observed lengths (B) with 95% confidence intervals for Bona, 2001. Minimum temperatures (T_{min}) and optimum temperatures (T_{opt}) for age-0 Arctic grayling.

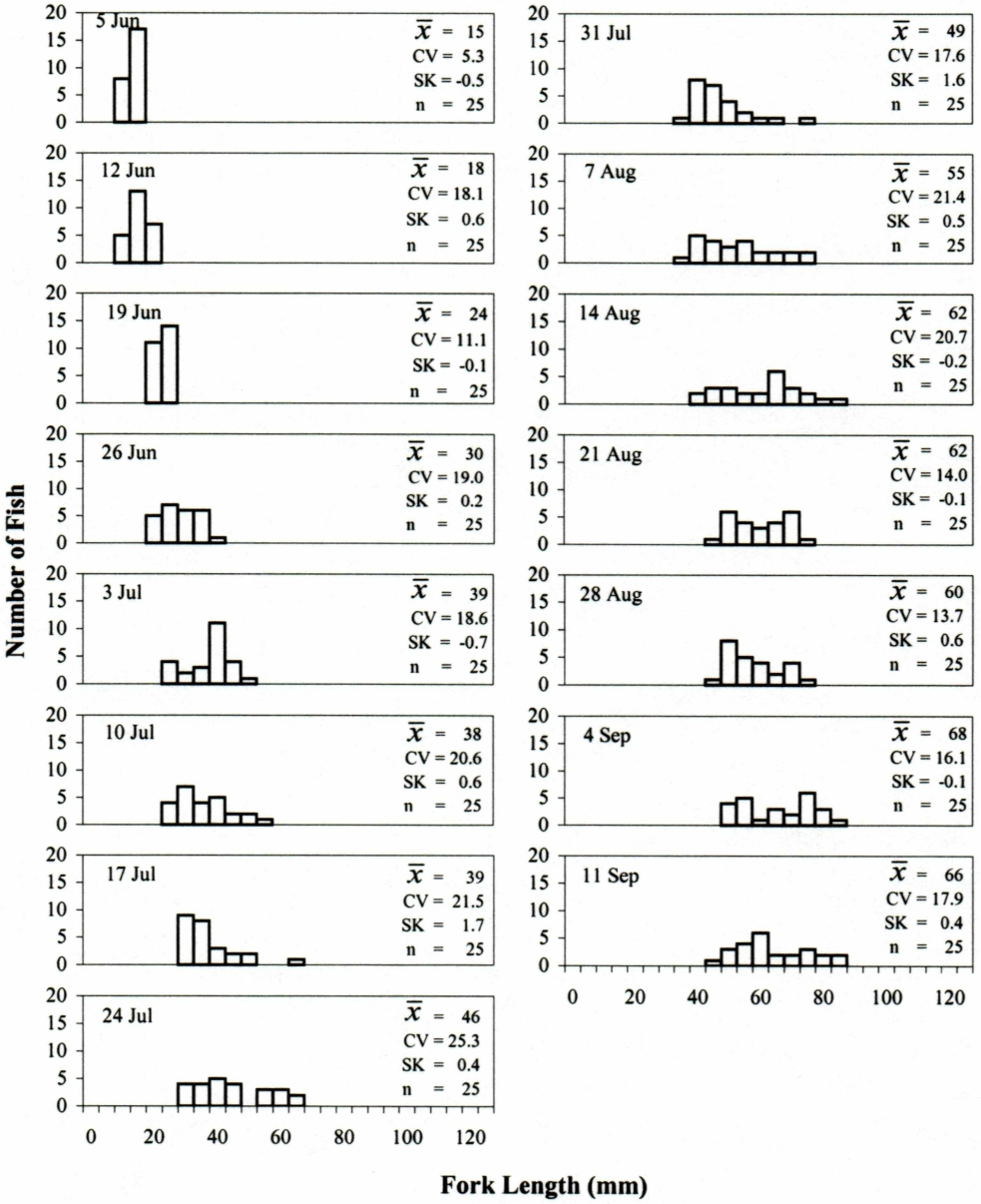

Figure 9.-Length-frequency histograms (5 mm increments) by week of Arctic grayling sampled at Bona, 2000. Mean length ($\bar{x}$), coefficient of variation (CV), skewness (SK), and sample size (n).

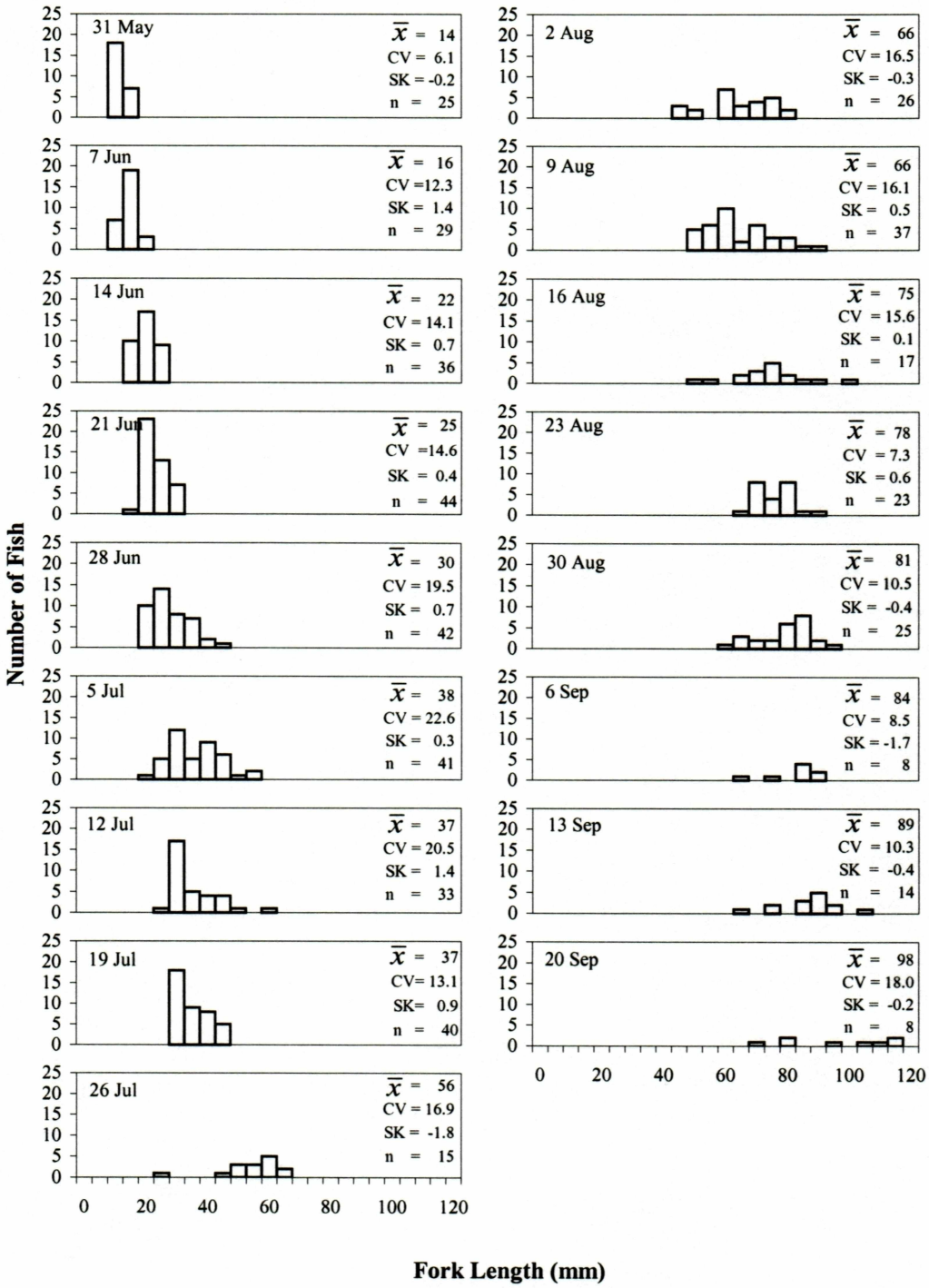

Figure 10.-Length-frequency histograms (5 mm increments) by week of Arctic grayling sampled at Bona, 2001. Mean length ($\bar{x}$), coefficient of variation (CV), skewness (SK), and sample size (n).

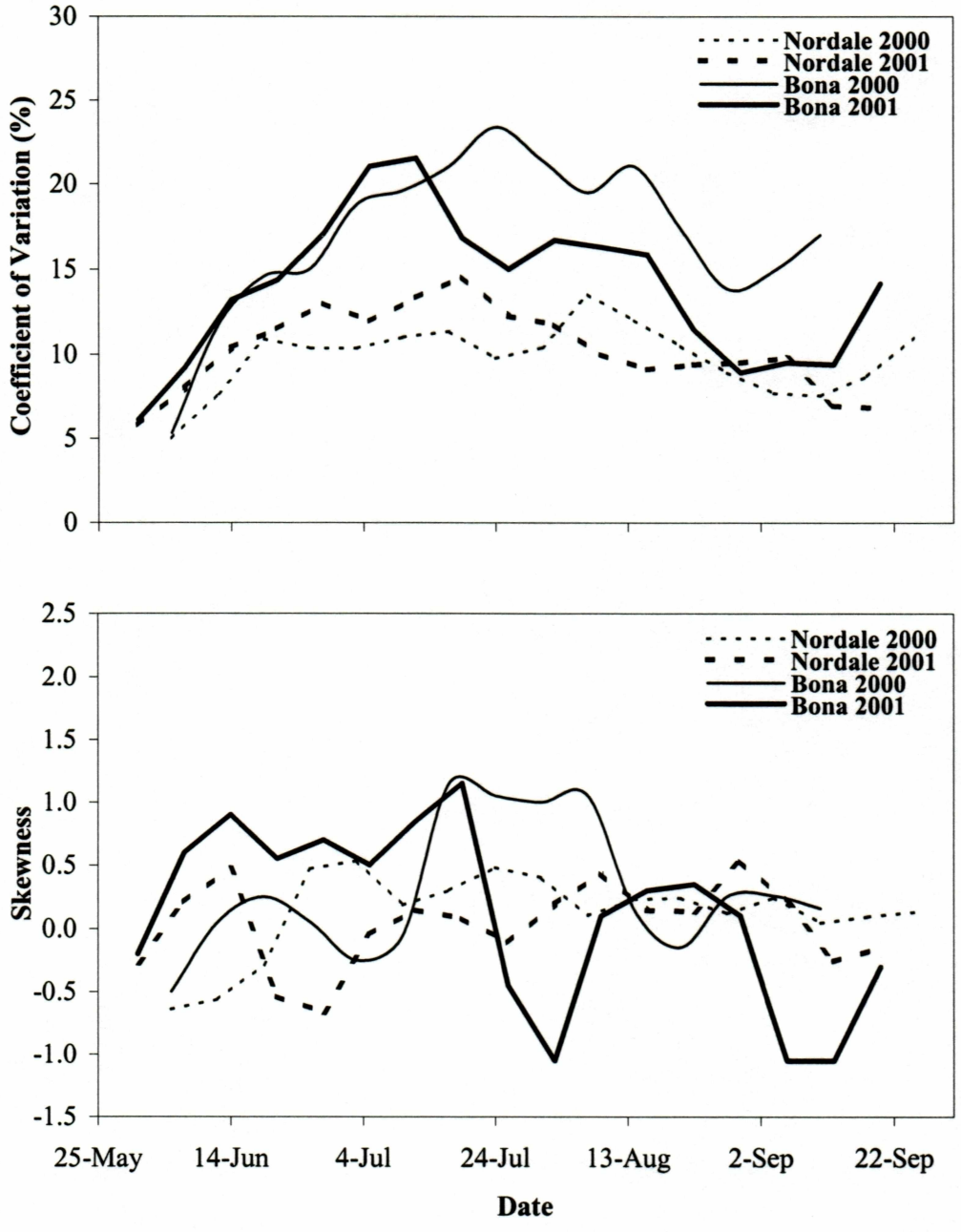

Figure 11.-Moving averages of the coefficient of variation (%) and skewness in lengths of Arctic grayling sampled at Nordale and Bona, 2000 and 2001.

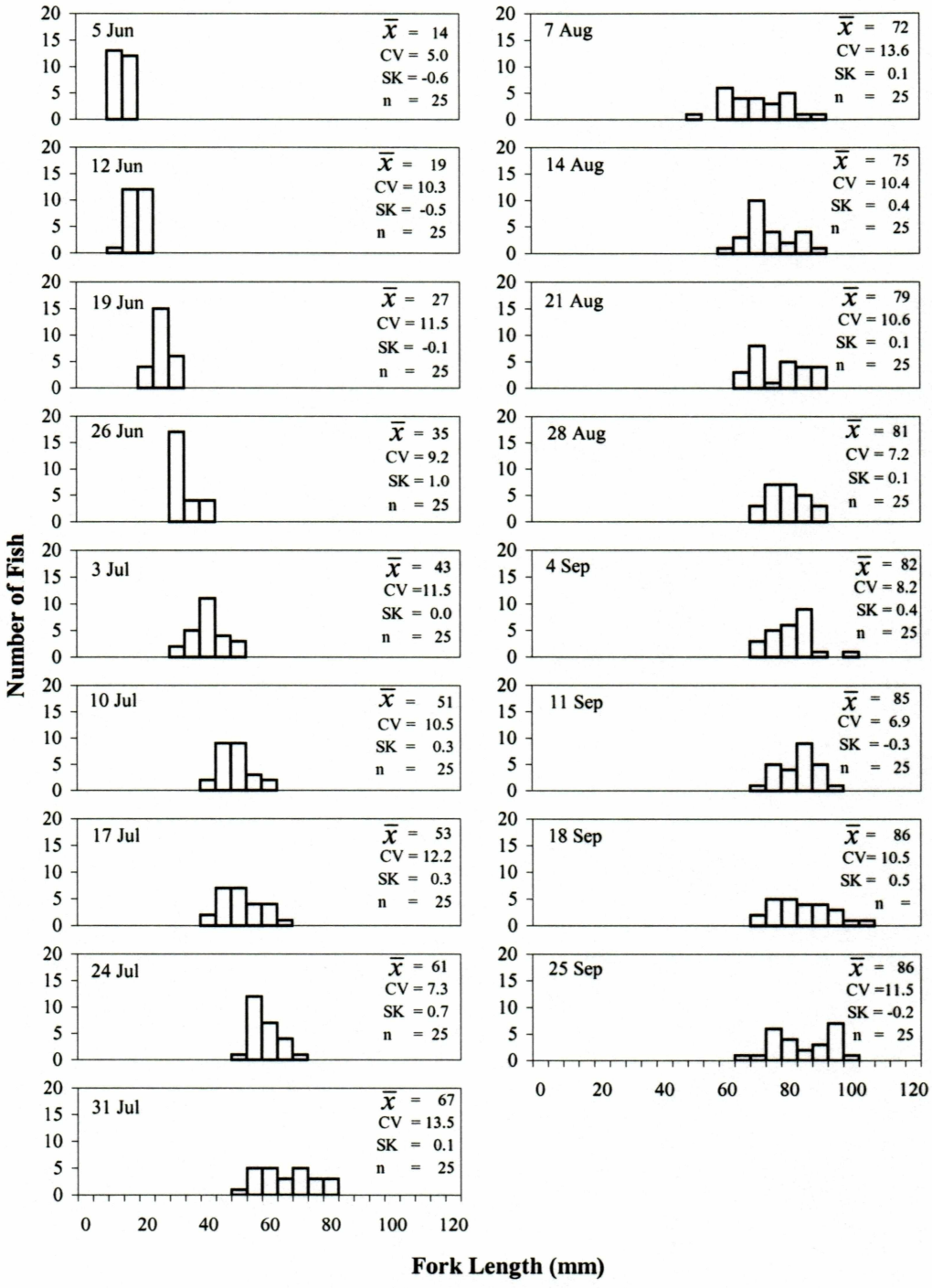

Figure 12.-Length-frequency histograms (5 mm increments) by week of Arctic grayling sampled at Nordale, 2000. Mean length ($\bar{x}$), coefficient of variation (CV), skewness (SK), and sample size (n).

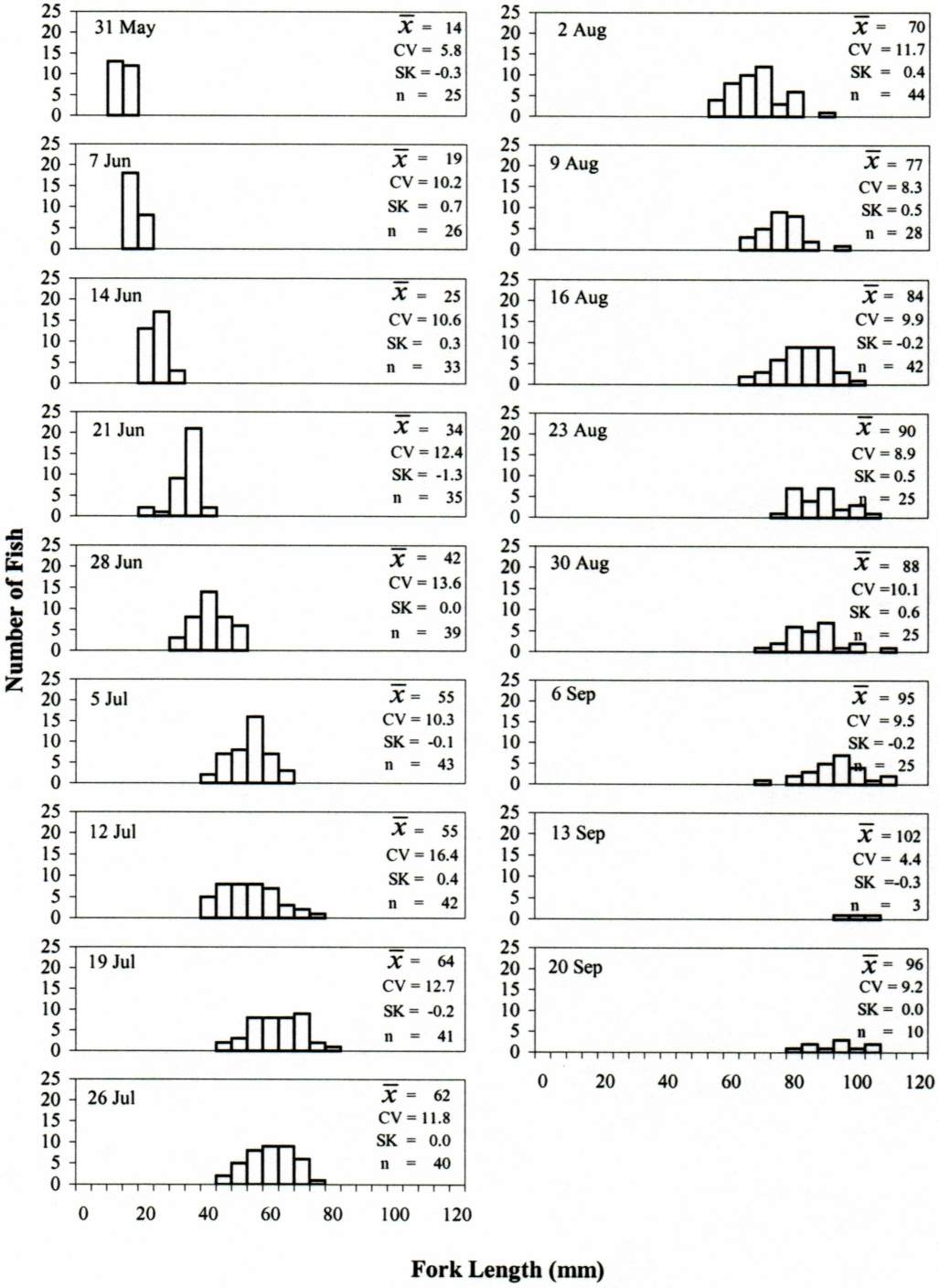

Figure 13.-Length-frequency histograms (5 mm increments) by week of Arctic grayling sampled at Nordale, 2001. Mean length ($\bar{x}$), coefficient of variation (CV), skewness (SK), and sample size (n).

Discussion

My results show that the Mallet et al. (1999) temperature-based growth model for European grayling accurately predicts growth rate of age-0 Arctic grayling at the Nordale reach but not at Bona. At Nordale the model made accurate predictions of length throughout each year of the study and also explained differences in growth rates between years.

The finding that growth was lower than predicted at Bona suggests that competition for food may be limiting growth. The departure of observed and predicted lengths suggests a decline in per-capita resource abundance. A conclusion that is consistent with the increase in CV of length and positive skewness in length during this time period. Indicating that Arctic grayling resemble steelhead trout (Keeley 2001) rather than brown trout (Elliott 1984a, 1984b, 1987; 1988; 1989a, 1989b, 1989c; 1990; 1994). These results demonstrate that the predictions of the model can be used to determine the timing of critical periods or bottlenecks that might influence year-class strength. My results indicate that a possible critical period or bottleneck occurred between weeks 4 and 7 at Bona, but not at Nordale.

The existence of this hypothesized critical period is consistent with a dramatic decline in fish abundance that occurred at Bona during mid July (personal observation), suggesting that this period of low growth is accompanied by density-dependent mortality or emigration (Elliott 1984a, 1984b; 1986; 1994). At Nordale there was actually an increase in fish abundance (personal observation) during this same time period, suggesting immigration and the absence of severe competition for space or food.

The hypothesized critical period at Bona corresponds with the time fish would shift from marginal areas to deeper, faster water, suggesting that Bona has high quality larval habitat but poor quality habitat for larger fish. In contrast Nordale appears to provide more than adequate amounts of high quality habitat for fish as they move from marginal habitats to deeper, faster water.

Fish at Bona appeared to show compensatory or recovery growth, indicated by the rapid increase in growth following the hypothesized bottleneck (Jobling 1994). The intensity and duration of a critical period can influence growth during the recovery period (Jobling 1994). This suggests that competition in 2000, when fish did not catch up with the predicted growth curve, may have been more intense than in 2001. However, in 2000 fish appeared to be more abundant following the critical period than in 2001, indicating higher survival rates or lower emigration in 2000. These higher densities following the critical period may actually account for slower growth rates during 2000.

The fact that a model developed for European grayling worked well for Arctic grayling, was surprising and it suggests that *Thymallus* species do not increase maximal growth rates with latitude to compensate for the shorter growing season (countergradient growth), or have genotypic differences in growth, as suggested by Conover (1990). Nor do they appear to exhibit variations in growth response to temperature with latitude as suggested by Jensen (1990) and Lobón-Cerviá and Rincón (1998).

My results showed that the Mallet et al. (1999) growth model could serve as a valuable tool for assessing thermal habitat quality for age-0 Arctic grayling. They also demonstrated that a comparison of observed and predicted growth curves can be used to detect the timing of food limitation and possible critical periods where density-dependent mortality or emigration can act to determine year-class strength.

CHAPTER 2: Testing The Ability of a Foraging Model to Predict Prey Size Composition of Age-0 Arctic Grayling in a Small Stream in Interior Alaska

Abstract

I evaluated the ability of a foraging model (Hughes and Dill. 1990. Can J. Fish Aquat. Sci. 47:2039-2048) to predict size composition of the diet for age-0 Arctic grayling *Thymallus arcticus*. Model predictions were initially poor but improved over the summer. The model overestimated mean prey length, but made accurate predictions of minimum lengths. Predicted maximum prey lengths were well above observed maximum lengths. In one reach the model correctly predicted a decline in mean prey size. In the other, it failed to predict an initial increase in prey size but correctly predicted no increase in size. High concentrations of suspended detritus may have made it difficult for fish to detect prey, causing them to restrict their reaction volume in order to reduce demands on their information processing capacity. This would reduce selectivity for large prey, violating the model's assumption of a linear relationship between prey length and reaction distance.

Introduction

Foraging models have been widely used to predict the size composition of prey in fish diets from size composition and abundance of prey in the environment (Werner and Hall 1974; Wańkowski 1979; Eggers 1982; Dunbrack and Dill 1983; Wright and O'Brien 1984; Grant and Noakes 1986; Rincón and Lobón-Cerviá 1999). Typically, the key component of these models is a positive relationship between reaction distance or reaction volume and prey size (Wańkowski 1979; Luecke and O'Brien 1981), this translates into predictions that fish will feed selectively on larger prey. Some of these models also use gill raker spacing and maximum mouth gape to establish the upper and lower limits of predicted prey size (e.g. Wańkowski 1979; Hayes et al. 2000).

In general, tests of these foraging models with drift-feeding salmonids have shown that they can accurately predict the size composition of the diet (Dunbrack and Dill 1983; Grant and Noakes 1986; Rincón and Lobón-Cerviá 1999). However, in some situations these models cannot account for observed selection behavior. For example, Rincón and Lobón-Cerviá (1999) found, contrary to model predictions, that brown trout *Salmo trutta* in a Spanish stream selected small invertebrates from the surface drift and ignored larger ones. They suggested that perceptual/cognitive limitations and energetic considerations interacted to determine prey selectivity. When large prey are rare and small prey are abundant, it may not be profitable for fish to attend to large prey items, as this may reduce their detection probability for more numerous small prey. Farell and Pelli's (1993) experimental study supports this

hypothesis with evidence that detection probability can decline when a predator attends to more than one prey size.

The purpose of this study was to establish whether a foraging model developed by Hughes and Dill (1990) and Hughes (1998) could be used to estimate the profitability of foraging habitat for juvenile rearing.

My objective was to test whether the model could accurately predict the size composition of the diet of age-0 Arctic grayling *Thymallus arcticus*.

Foraging Model

The original model designed by Hughes and Dill (1990) and Hughes (1998) is a geometrical depiction of the manner in which the foraging capabilities of drift-feeding fish interact with the physical environment to determine the net rate of energy intake for the fish. For model assumptions and original equations see Hughes and Dill (1990) and Hughes (1998). A geometric illustration depicting Arctic grayling food capture area is shown in Figure 14.

I modified the model by adding constraints on minimum and maximum prey lengths and developed a new equation for the relationship between fish size and maximum sustainable swimming speed (VMAX) to correspond with the smaller fish used in my study.

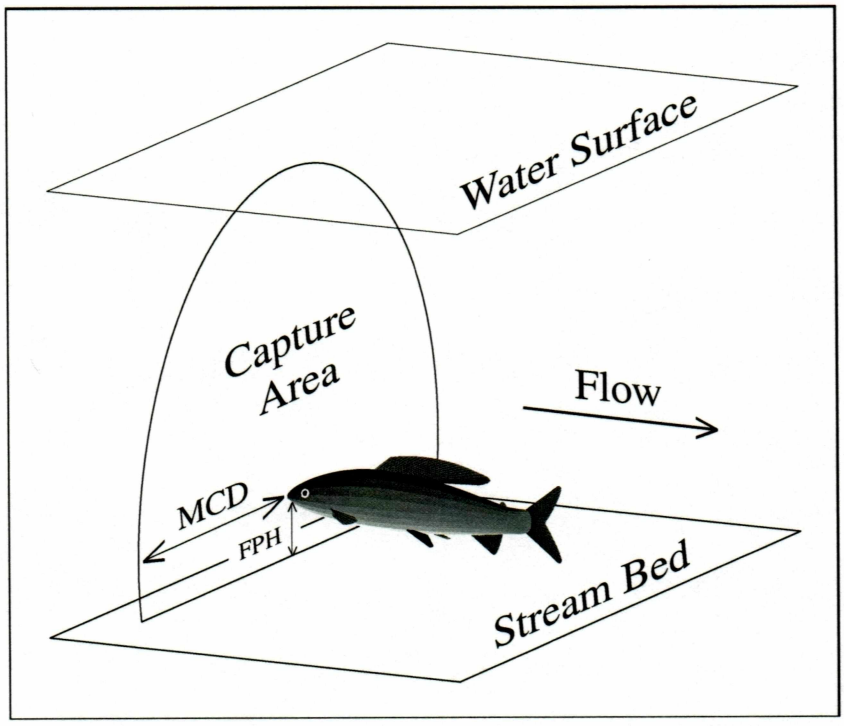

Figure 14.-Illustration depicting a food capture area for Arctic grayling. MCD is the maximum lateral capture distance and FPH (cm) is the focal point height of the fish from the streambed. Fish are assumed to select positions where depth and velocity maximize the rate which prey pass through its capture area. Modified from Hughes (1998).

Methods

Data Collection

I sampled invertebrate drift and collected age-0 Arctic grayling for diet analysis from both study reaches in 2000 to test the model's ability to predict the length-frequency distribution of prey in the diet. Drift and fish samples were collected on 21 June, 18 July and 14 August at Nordale and on 22 June, 19 July and 14 August at Bona. All samples were collected around noon.

I positioned two 0.10 m wide (0.0234 m^2 mouth area) x 1.0 m long cone-shaped drift nets at the top of each study reach with the mouth edge just above the stream bed, to establish invertebrate drift density and size composition. I used 80 μm mesh size in June and 153 μm mesh size in July and August. Sampling periods at Nordale were 10 min in June and July, and 60 min in August. Sampling periods at Bona were 10 min in June, 20 min in July, and 60 min in August. I measured water velocity at the center of each net opening with a Marsh-McBirney Model 2000 portable current meter set to average over 40 s, at the beginning and end of each sampling period. I averaged the two readings to get mean velocity for the sample period to determine volume of water filtered.

I collected five fish from each reach at the same time drift was sampled to establish the size composition of the diet. All fish and drift samples were preserved in 70% ethanol for lab analysis.

Later, in the lab, I counted, identified, and measured organisms in the drift samples and intact prey items from the stomachs using a microscope-digitizing program

(ZoopBiom 2.0) developed by Russell Hopcroft (unpublished). I identified invertebrates to family when possible, using keys in Merritt and Cummins (1996) or Pennak (1989). Prey biomass (mg) was determined using general length-dry mass relationships for insects (Smock 1980) and zooplankton (Russell Hopcroft, personal communication).

I measured the spacing of gill rakers on the first gill arch from a sample of 6 fish collected from Nordale for diet determination, to establish a relationship for minimum prey length.

Analysis

I compared the amount of unexplained variation (*UV*) left by the model to the variation left unexplained by a null model (*Observed vs. Drift*) of non-selective predation, in which the fish ate prey in different size-classes in the same proportion that they occurred in the drift, to assess how accurately the foraging model predicted the observed length-frequency of the diet. Under the null model the length frequency of prey in the diet should be the same as the length-frequency of organisms in the drift. I calculated the sum of squares of error (*SSE*) between the proportion of each size-class in observed and predicted diets and between observed diets and drift. The percentage of variation left unexplained by the null model of non-selective predation that is explained by the foraging model is then:

$$(1) \qquad UV = (SSE_{\text{Observed vs. Drift}} - SSE_{\text{Observed vs. Predicted}}) \,/\, (SSE_{\text{Observed vs. Drift}}) \cdot 100$$

Note that when the null model works better than the foraging model this percentage will be negative, indicating that the null model makes more accurate predictions of the diet than the foraging model.

I examined the relationship between fish length and the observed minimum, mean, and maximum prey lengths and compared these observations to the model's predictions of minimum, mean, and maximum prey lengths, to further test how well the foraging model was able to predict the prey sizes consumed by the fish.

I established a relationship for fish size and minimum prey length by regressing mean gill raker spacing on fish length to obtain the equation: Minimum prey length = 0.0046·fish fork length. I used the relationship that Hayes et al. (2000) developed from Wańkowski (1979) for maximum prey length: Maximum prey length = 0.452·fish fork length.

I developed a new equation for the relationship between fish size and maximum sustainable swimming speed (VMAX) to provide a better estimate of the relationship for small fish. I fit a polynomial function to data on the maximum sustainable swimming speed of age-0 European grayling *Thymallus thymallus* (Scott 1985) to obtain the equation: $VMAX = -0.462 + 1.019 \cdot (1 - e^{(-54.4 \cdot \text{fish length})})$. This relationship is suitable for Arctic grayling between 14 mm and 100 mm in length.

Results

Length-frequency distributions of invertebrates in the drift, observed diet, and predicted diet for Nordale are shown in Figure 15. The foraging model explained 33%,

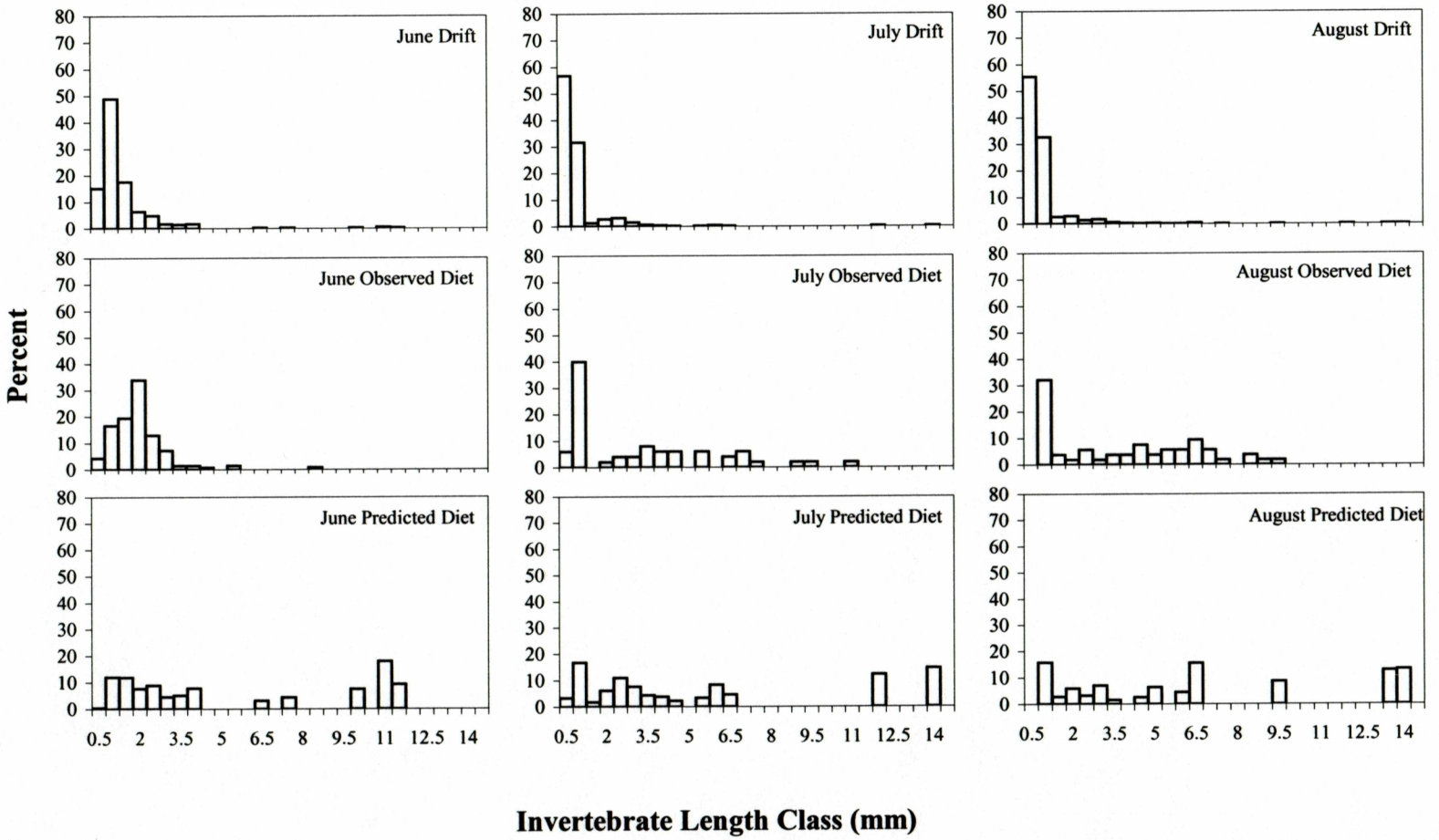

Figure 15.-Histograms of the percent of invertebrates in each length-class (5 mm increments) for predicted and observed Arctic grayling diets and observed drift at Nordale, 2000.

60%, and 85% of the variation left unexplained by the null model in June, July, and August respectively.

Invertebrate length-frequency distribution results for Bona are shown in Figure 16. The foraging model explained -50%, -33%, and 57% of the variation left unexplained by the null model in June, July, and August respectively.

Model predictions of mean prey length were consistently too large in both reaches, falling at the upper end of the range for observed mean prey lengths (Figures 17 and 18). At Nordale the model predicted that mean prey size would be relatively stable over the summer at about 5.4 mm, yet prey size actually increased from about 1 mm to 6 mm as fish grew. At Bona observed mean prey size decreased from about 4 mm to1 mm over the summer and the model accurately accounted for this decline yet overestimated the lengths (6 mm to 3 mm). The model's gill raker spacing constraint led to accurate predictions of the observed minimum prey size and the maximum observed prey size fell progressively further below the limit set by mouth gape as the summer progressed and fish grew.

Data on drift characteristics are summarized in Table 2. Drift densities (number$\cdot m^3$) at both reaches were high in June but decreased to only 20% of initial values by August. Bona had higher drift densities than Nordale in June and August, but densities were similar in July. The mean length of drifting invertebrates fell from 1.68 mm in June to 0.47 mm in August at Bona and from 1.15 mm to 0.73 mm at Nordale.

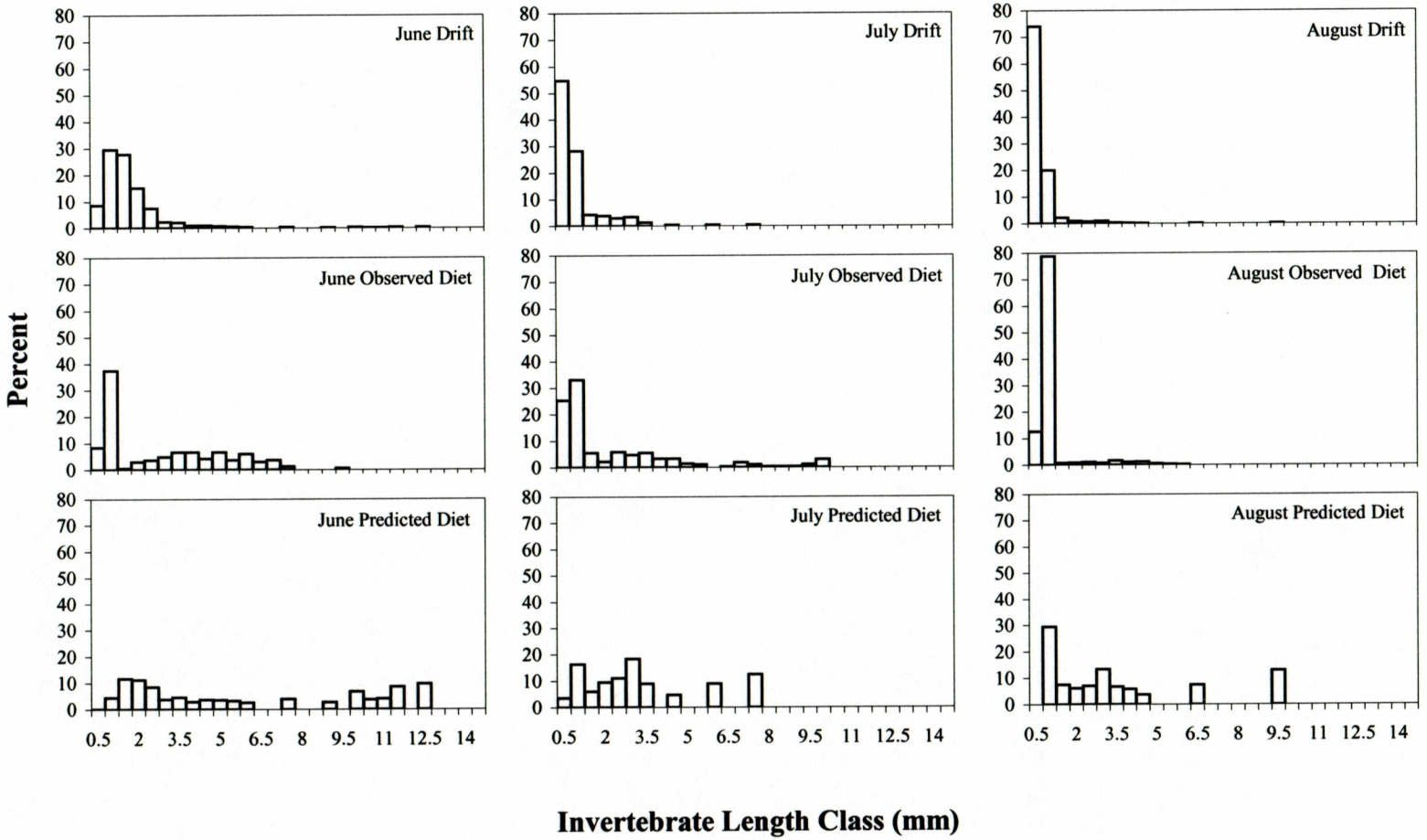

Figure 16.-Histograms of the percent of invertebrates in each length-class (5 mm increments) for predicted and observed Arctic grayling diets and observed drift at Bona, 2000.

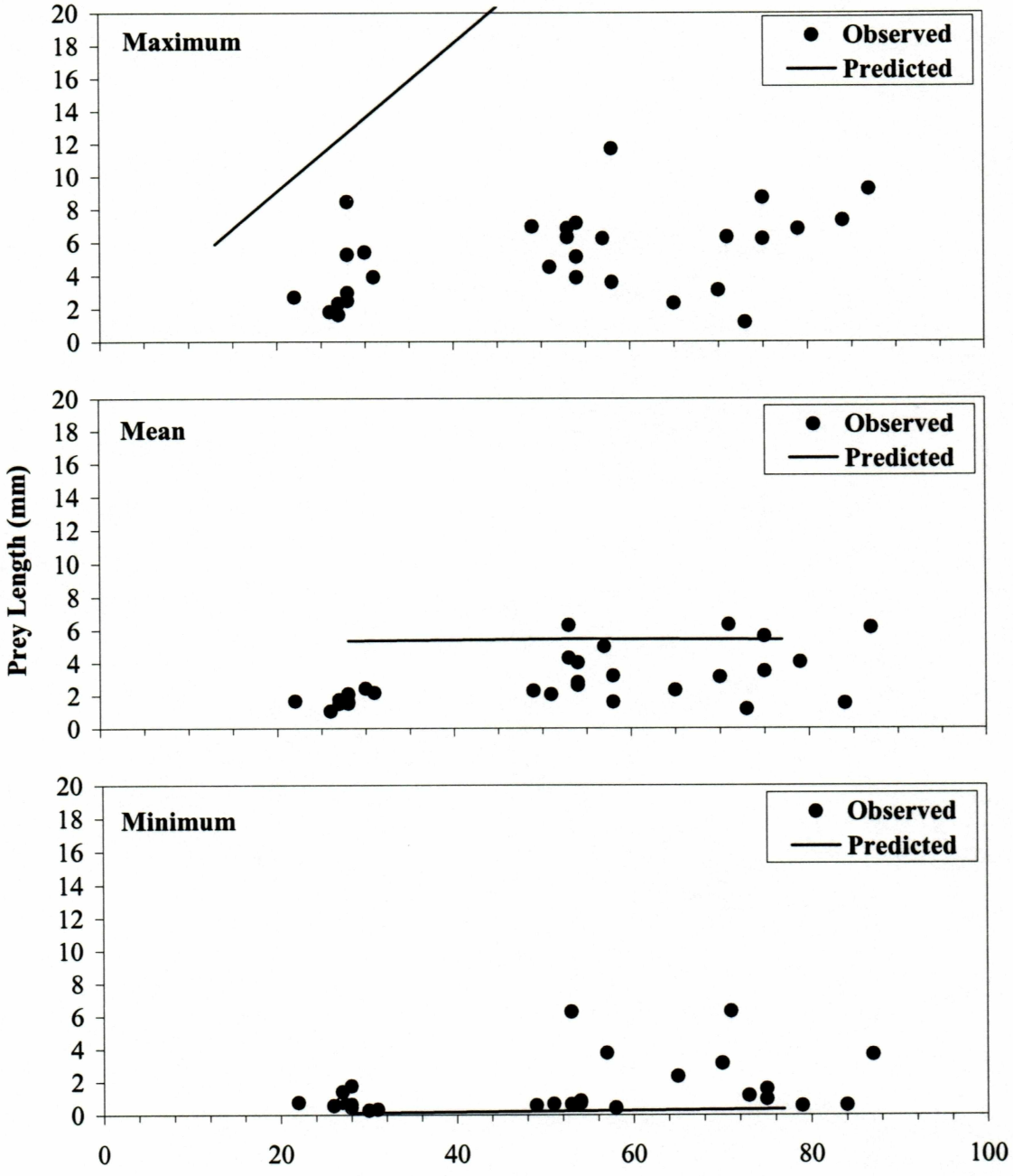

Figure 17.-Maximum, mean, and minimum prey lengths (mm) of Arctic grayling sampled at Nordale, 2000.

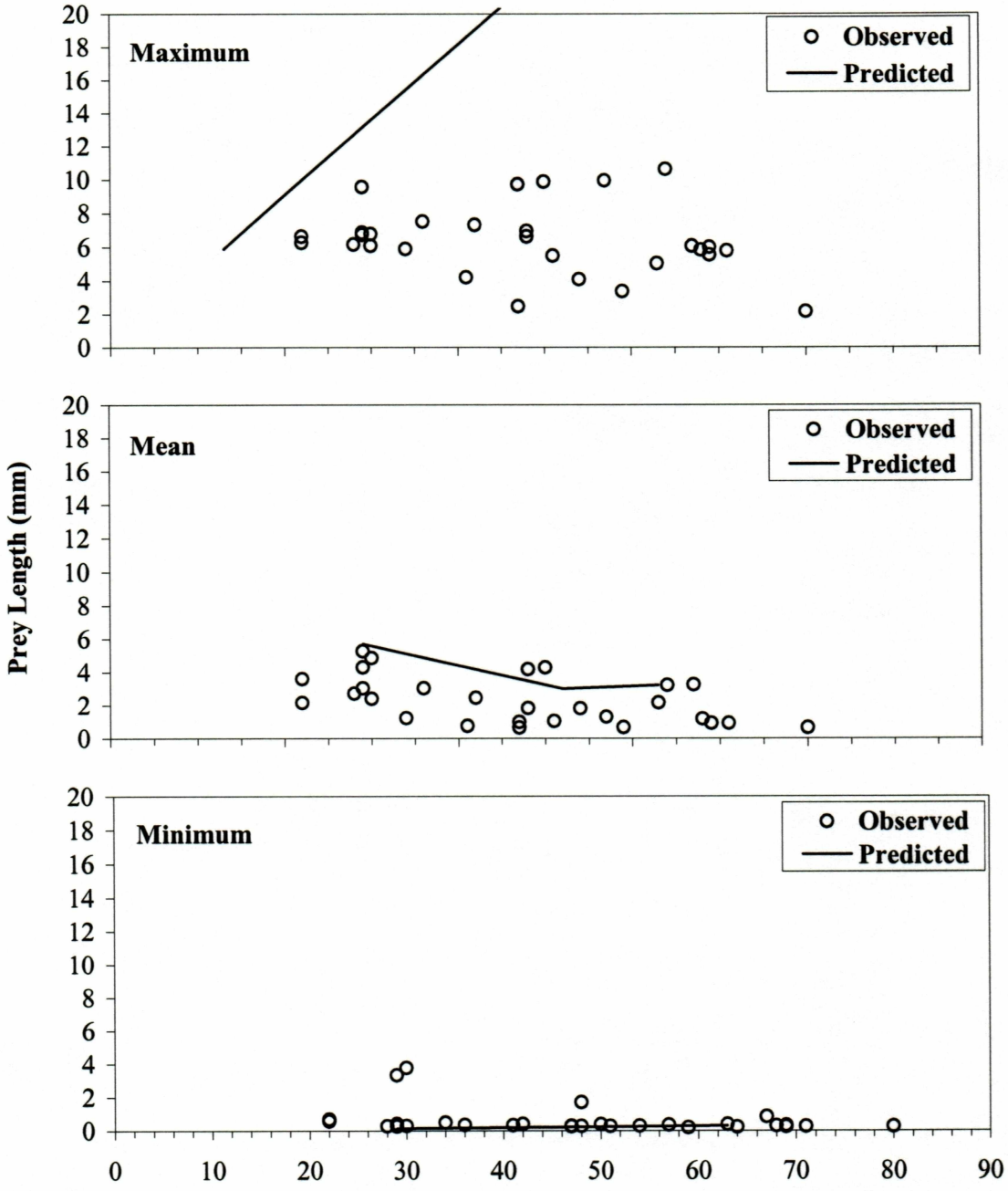

Figure 18.-Maximum, mean, and minimum prey lengths (mm) of Arctic grayling sampled at Bona, 2000.

Table 2.-Average drift density (number·m^3) with 95% confidence intervals at Nordale and Bona, 2000. (—, no data).

Nordale	Net	Weighted mean length (mm)	Drift density (number·m^3)	Average drift density (number·m^3)
June	1	1.15	47.78	44.60 ± 6.23
	2		41.42	
July	1	0.72	33.39	33.65 ± 0.52
	2		33.92	
August	1	0.73	8.24	8.68 ± 0.86
	2		9.12	
Bona				
June	1	1.68	58.57	69.01 ± 20.47
	2		79.46	
July	1	0.76	25.18	30.29 ± 10.03
	2		35.41	
August	1	0.47	16.27	16.27
	2		—	

The main taxa in the drift at Bona were small Chironomidae, Ostracoda and Chydoridae (Table 3). Simuliidae were the dominant taxa in the diet during June and Ostracoda during July and August. Ostracoda and Copepoda were consistently abundant in the drift at Nordale, yet Chironomidae were dominant in the diet during June and July, and Baetidae during August (Table 3).

Discussion

The foraging model's predictions of the length-frequency of the diet of age-0 Arctic grayling were inaccurate early in the season but improved as fish grew. By August the model was able to explain 85% of the variation left unexplained by a null model of unselective predation at Nordale and 57% at Bona. However, the negative numbers in June and July at Bona show that the null model of unselective predation was a better predictor of the length-frequency in the diet than the foraging model. These predictions are poor compared to other studies where similar models have been used to predict the size composition of the diet. For example, the model tested by Dunbrack and Dill (1983) is conceptually similar to Hughes and Dill (1990), and explained 98% of the variation in the diet of drift-feeding coho salmon *Oncorhynchus kisutch* compared to a model of unselective predation. The poor performance of the model in this study is largely due to the fact that it was unable to predict the number of small prey consumed. Perhaps the most likely explanation for the model's inability to predict small prey is that large quantities of suspended detritus in Chena Slough may make it

Table 3.-Summary of the most abundant taxa (%) in Arctic grayling diets and invertebrate drift at Nordale and Bona, 2000. (—, no data)

	Nordale		Bona	
Sample date	Taxa	% of drift	Taxa	% of drift
June Net 1	Chironomidae	32	Chironomidae	74
	Copepoda	40	Ostracoda	9
June Net 2	Chironomidae	39	Chironomidae	65
	Copepoda	39	Ostracoda	13
July Net 1	Copepoda	31	Copepoda	17
	Ostracoda	47	Ostracoda	38
July Net 2	Copepoda	31	Copepoda	15
	Ostracoda	50	Ostracoda	44
August Net 1	Chydoridae	28	Chydoridae	58
	Ostracoda	42	Ostracoda	20
August Net 2	Chydoridae	22	—	—
	Ostracoda	44	—	—

harder for Arctic graying to detect prey. O'Brien and Showalter (1993) showed that stream detritus caused Arctic grayling to narrow the width of their reaction volume. They hypothesize that this narrowing is a response to increased information processing demands associated with discriminating prey from detritus. Drift feeding fish may also narrow their search window in response to high prey abundance (Ringler 1979) and this may be occurring in Chena Slough, especially early in the summer (Table 1). If fish narrowed their reaction volume for either reason, it would condense the reaction volume predicted by the model and reduce selectivity for large prey.

The dramatic decrease in mean length of organisms at Bona may be attributed to the increasing abundance of Ostracoda in the drift over the course of the summer. The more stable prey length and weights observed at Nordale can be attributed to the presence of Baetidae. Although, Ostracoda were also numerous throughout the summer, and Chironomidae were abundant early in the summer but became more rare as the summer progressed.

The observation that the model worked increasingly well as the summer progressed and fish grew may be a consequence of the fish's ability to discriminate prey from detritus more accurately as their foraging and visual capabilities improve (McLaughlin et al. 2000). As a result of these changes, Arctic grayling might progressively expand the boundary of their search area. This would increase the reaction volume predicted by the model and, because fish behavior would closely approximate model assumptions, we might expect the model's predictions to improve. Reduced prey densities may also favor an expansion of the fish's search area (Ringler

1979) and it is also possible that an increase in maximum ration size as fish grew may have been responsible for an expansion of the reaction volume towards the theoretical limits.

Another explanation for the model's inability to predict small prey is that Arctic grayling in Chena Slough are selectively attending to small prey in response to perceptual limitations as suggested by Rincón and Lobón-Cerviá (1999). This might involve the formation of a "search image", where an individual focuses its attention on detecting small prey (Dukas and Ellner 1993) or specialization of individual fish on particular taxa (Allen 1941; Bryan and Larkin 1972; Bisson 1978; Ringler 1985). Existing models for drift-feeding fish cannot explain patterns of prey selection, although these hypotheses provide a theoretical foundation for thinking about the problem.

Drift prey abundance does not appear to be a limiting factor for growth of juvenile Arctic grayling. However, drift may only be representative of what remains after fish have eaten selected prey items (Allan 1984) or spatial variation in drift size composition and taxa may be occurring because of substrate differences throughout the reaches.

My results indicate that Arctic grayling in Chena Slough appear to be narrowing the size of their reaction volume, focusing on small prey items, possibly in response to suspended stream detritus that may be inhibiting their visual capabilities. Stream detritus has not been given enough consideration and should be integrated into models that make assumptions about fish prey detection, interception, capture area and reaction volume.

CHAPTER 3: Predicting Distribution Patterns and Ontogenetic Habitat Shifts of Age-0 Arctic grayling in a Small Stream in Interior Alaska

Abstract

I evaluated the ability of a habitat selection model (Hughes and Dill. 1990. Can J. Fish Aquat. Sci. 47:2039-2048) to predict the distribution and ontogenetic habitat shifts of age-0 Arctic grayling *Thymallus arcticus* within two reaches of a nursery stream. I also applied the logic of Ideal Free Distribution Theory (IFD) to predict relative abundance in the distribution of fish between the two reaches. Within each reach the model made accurate predictions of the distribution of larval fish, and the shift to faster, deeper water as fish grew. However, detailed predictions of the distribution of larger fish were not as accurate; many fish occupied positions in faster, shallower water than predicted by the model. The IFD approach accurately predicted the relative abundance of fish between reaches, including a shift in maximum fish density from the upstream reach to the downstream reach early in the season.

Introduction

Habitat selection models are increasingly being used to predict fish distribution and assess habitat quality (Fausch1984; Hughes and Dill 1990; Hill and Grossman 1993; Heggenes and Saltveit 1996; Baker and Coon 1997; Braaten et al. 1997; Guay et al. 2000; Nislow et al. 2000; Porter et al. 2000; Boisclair 2001; Guensch et al. 2001; Rosenfeld and Boss 2001; Tyler and Brandt 2001). The benefit of this approach is that models that integrate physical and biological habitat characteristics such as water depth, velocity, temperature and prey abundance into a single biologically meaningful estimate (e.g. rate of energy intake or growth rate potential), allow them to functionally define habitat quality with respect to the physiological needs of the fish.

Habitat selection models for drift-feeding salmonids have been successful at predicting the distribution of fish within a reach (Hughes and Dill 1990; Hill and Grossman 1993; Guensch et al. 2001) and the way seasonal changes in flow, food abundance, and water temperature affect juvenile fish abundance within a stream reach via their influences on habitat availability (Nislow et al. 2000). These applications suggest that habitat models have considerable promise as habitat assessment tools and can provide insight as to how physical and biological changes to streams may impact salmonid populations.

Despite the success of these models for drift-feeding fish they have not yet been applied to predict habitat selection of very small salmonids or ontogenetic habitat shifts to faster, deeper water, which is typical of salmonids in early developmental stages (Everest and Chapman 1972; Keeley and Grant 1995). Ontogenetic or size related

shifts in habitat often occur as individuals increase in body size and enhance their foraging capabilities (Mittelbach 1981; Sempeski and Gaudin 1996). Existing habitat selection models for drift-feeding salmonids should be capable of making these predictions because they incorporate size-dependent relationships for the fish's visual capabilities, swimming abilities, and constraints on maximum and minimum prey size (e.g. Hughes and Dill 1990; Hayes et al. 2000).

To date, researchers have focused on the ability of these models to predict distributions within a reach but they have not been developed to predict distribution between reaches, something that might be attempted by integrating predictions from these models with Ideal-Free Distribution (IFD) theory. According to IFD theory (Fretwell and Lucas 1970), fish should, in an attempt to maximize fitness, distribute themselves such that the proportion of individuals in each habitat matches the proportion of available resources. Thus, fish distribution between reaches should reflect differences in resource renewal rates (Power 1984; see also Grand 1997; Grand and Dill 1997; Hughes and Grand 2000).

The purpose of this study was to evaluate whether a habitat selection model developed by Hughes and Dill (1990) and Hughes (1998) could be used to ascertain rearing habitat quality and differences in rearing quality between two reaches.

My first objective was to determine if the model could adequately predict stream reach distribution of age-0 Arctic grayling *Thymallus arcticus*, and ontogenetic habitat shifts during each developmental stage within a reach.

My second objective was to combine the predictions of the model with the logic of IFD theory to predict relative fish abundance between the two reaches.

Habitat Selection Model

The habitat selection model is a combination of a foraging model described by Hughes and Dill (1990) and a habitat selection model described by Hughes (1998). The model uses information on spatial variation in water depth, velocity and temperature, and the density and size composition of invertebrate drift to predict spatial variations in net rate of energy intake (NREI). The model assumes that fish will select profitable positions where the predicted NREI is high. A geometric illustration depicting Arctic grayling food capture area is shown in Figure 19. For complete model assumptions and equations see Hughes and Dill (1990) and Hughes (1998).

I modified the model by adding constraints on minimum and maximum prey lengths and developed a new equation for the relationship between fish size and maximum sustainable swimming speed (VMAX) to correspond with the smaller fish used in my study.

Methods

Data Collection

I mapped water velocity ($m \cdot s^{-1}$) and depth (m) on 26 June 2000 at Nordale and 27 June 2000 at Bona to obtain the physical habitat measurements needed for the

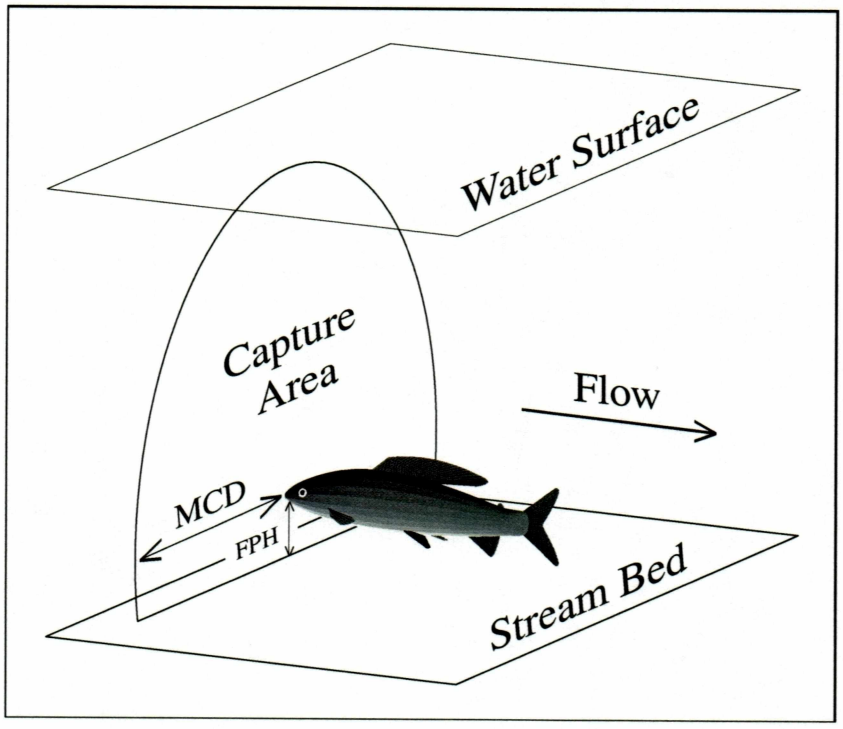

Figure 19.-Illustration depicting a food capture area for Arctic grayling. MCD is the maximum lateral capture distance and FPH (cm) is the focal point height of the fish from the streambed. Fish are assumed to select positions where depth and velocity maximize the rate which prey pass through its capture area. Modified from Hughes (1998).

model. I spaced transects (perpendicular to the flow, x-axis) at one m intervals, measuring depth and mean water velocity at 0.6 depth below the water surface every 1 m along each transect using a Marsh-McBirney Model 2000 portable current meter set to average water velocity over 40 s.

I conducted an underwater video survey using a Deep Sea Power and Light underwater video camera to determine spatial variation in fish density and distribution within- and between-reaches. The video camera was mounted on the end of a 4.6-m long piece of conduit to reduce fish disturbance and movement. The conduit projected from a custom made floating Styrofoam platform that carried a power supply and video monitor. I waded slowly up the reach pushing the platform and camera from side to side to provide video coverage of the entire stream bed. I surveyed each reach three times during the course of the summer, Nordale on 21 June, 18 July, and 16 August 2000, and Bona on 22 June, 19 July and 16 August 2000. I inserted small flat wooded stakes labeled with x, y coordinates into the stream bed on 1x1 m grids within each reach to provide a spatial reference when interpreting the video.

I measured fork length (mm) of fish weekly at both study reaches, from shortly after they emerged from the gravel, starting 5 June 2000, until the end of September to determine average monthly fish size for the model. A weekly sub-sample of 25 fish were sampled in 2000, all fish seined were sampled each week in 2001. Larval fish were collected using hand-held aquarium nets, and 3 mm mesh seines were used for larger fish. I anesthetized fish with clove oil (0.1 ml clove oil to 100 ml water) to facilitate accurate measurement.

I measured the spacing of gill rakers on the first gill arch from a sample of 6 fish collected from Nordale for diet determination, to establish a relationship for minimum prey length. I regressed mean gill raker spacing on fish length to obtain the equation: Minimum prey length = 0.0046·fish fork length. For maximum prey length I used the relationship that Hayes et al. (2000) developed from Wańkowski (1979): Maximum prey length = 0.452·fish fork length.

I also developed a new equation for the relationship between fish size and maximum sustainable swimming speed (VMAX) to provide a better estimate of the relationship for small fish. I fit a polynomial function to the data on the maximum sustainable swimming speed of age-0 European grayling *Thymallus thymallus* (Scott 1985) to obtain the equation: $VMAX = -0.462 + 1.019 \cdot (1 - e^{(-54.4 \cdot \text{fish length})})$. This relationship was established for Arctic grayling between 14 mm and 100 mm in length.

I used the maximum predicted NREI at each reach as an index of food input rate to predict the relative abundance of fish between reaches. According to IFD theory, fish should distribute themselves such that the ratio of fish abundance between reaches matches the ratio of input rates, termed "input-matching". I therefore hypothesized that fish would distribute themselves between reaches such that relative abundance of fish in each reach equaled the relative magnitude of maximal NREI in that reach.

Analysis

I plotted the observed patterns of fish distribution onto contour maps of depth, velocity and predicted NREI to assess the ability of the model to predict habitat

selection and ontogenetic habitat shifts within each reach. This allowed a simple visual assessment of the match between observed distributions and spatial variations in predicted NREI for each reach and sampling date.

I computed the ratios of fish abundance and maximal NREI between reaches to test whether the IFD theory and input-matching prediction could predict differences in the abundance of fish between Nordale and Bona. If the prediction worked, the ratio of maximal NREI between reaches and the ratio of fish abundance between reaches would be equal on all three-sample dates.

Results

Physical habitat characteristics and predicted NREI are compared to fish distribution patterns at Nordale in Figures 20, 21 and 22. Maximum depth was 0.40 m and maximum velocity was 0.79 m/s. Maximum predicted NREI for Nordale was 1.37 J/h in June, 5.47 J/h in July and 1.71 J/h in August. On 21 June 206 fish averaging 27 mm in length were observed along the margins, on 18 July 954 fish averaging 53 mm were observed throughout the entire reach, and on 16 August 372 fish averaging 75 mm were observed in moderately fast, deeper sections of the main channel.

Physical habitat characteristics and predicted NREI are compared to fish distribution patterns at Bona in Figures 23, 24, and 25. Maximum depth was 0.37 m and maximum velocity was 0.88 m/s. Maximum predicted NREI for Bona was 3.70 J/h in June, 0.51 J/h in July and 0.12 J/h in August. On 22 June 441 fish averaging 24 mm in length were observed along the margins, on 19 July 76 fish averaging 39 mm were

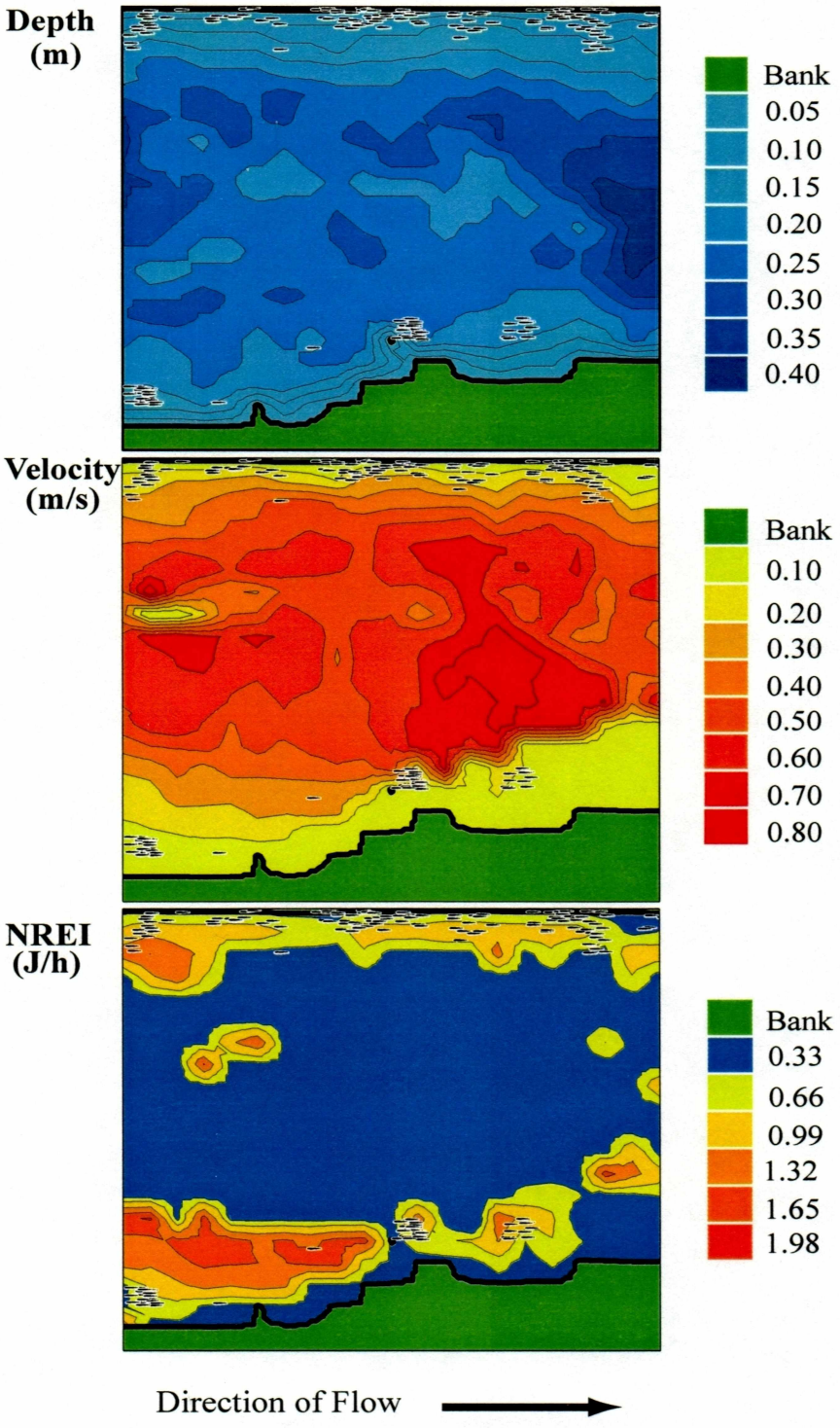

Figure 20.-Arctic grayling distribution maps showing depth, velocity and predicted net rate of energy intake (NREI) contours at Nordale, June 2000.

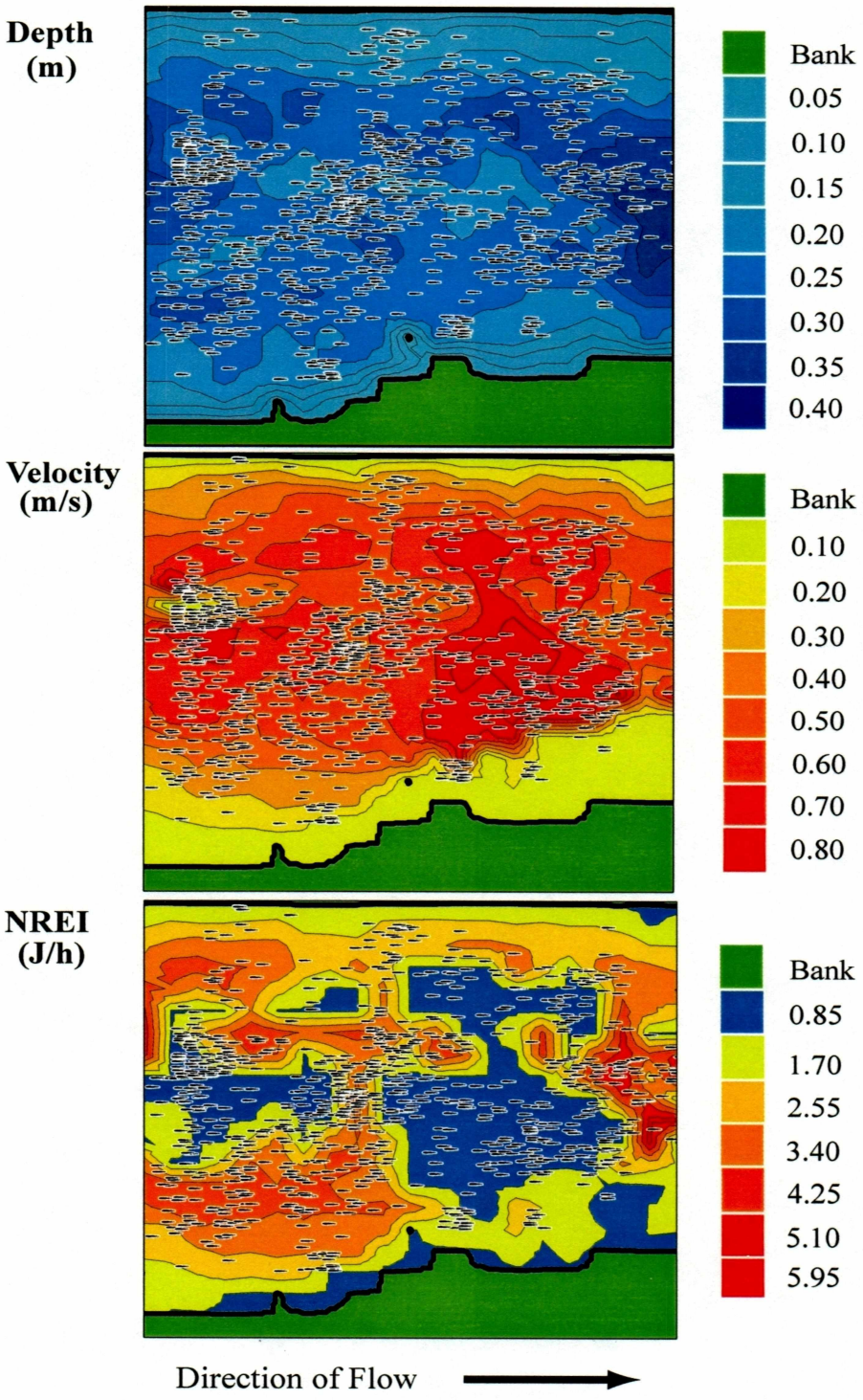

Figure 21.-Arctic grayling distribution maps showing depth, velocity and predicted net rate of energy intake (NREI) contours at Nordale, July 2000.

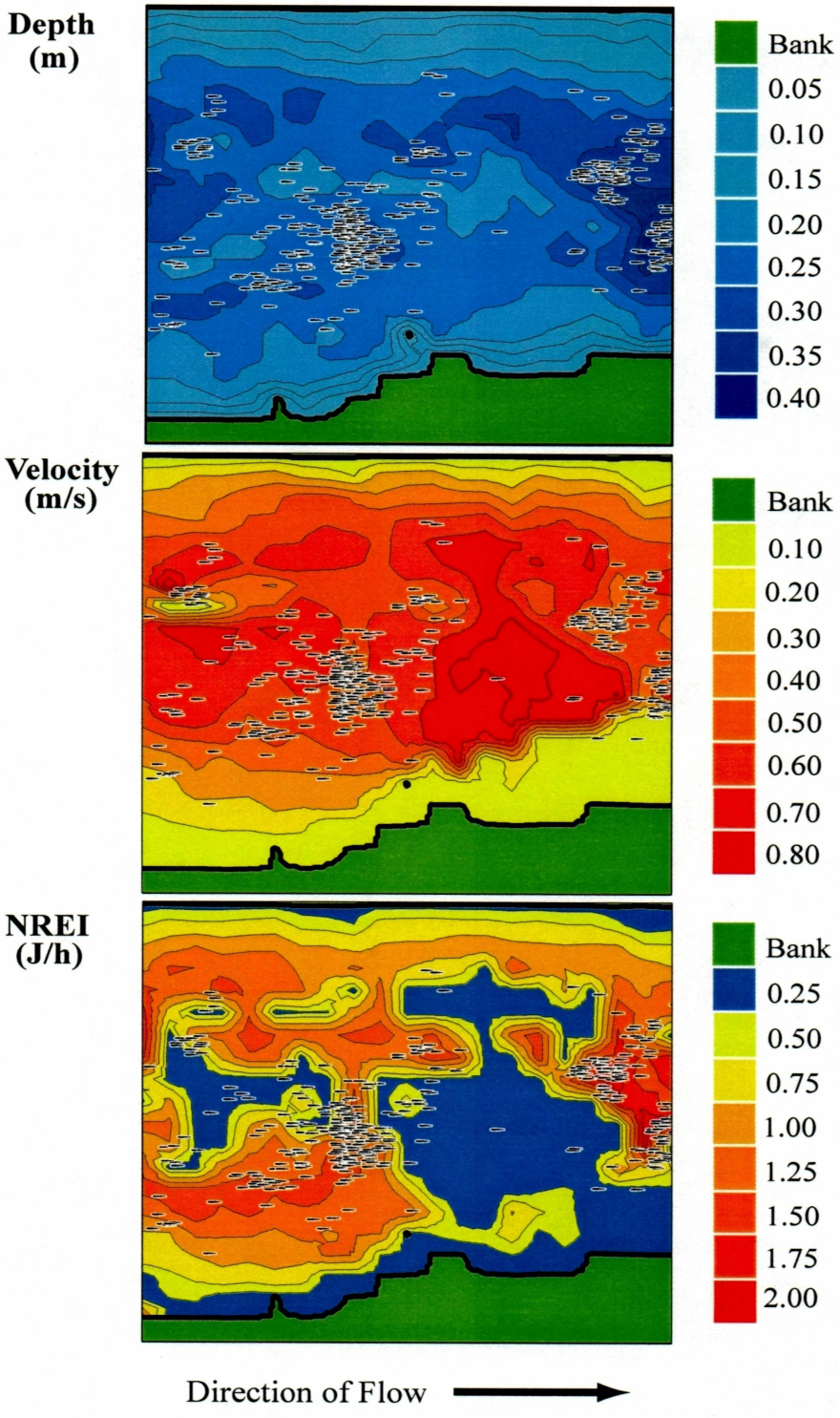

Figure 22.-Arctic grayling distribution maps showing depth, velocity and predicted net rate of energy intake (NREI) contours at Nordale, August 2000.

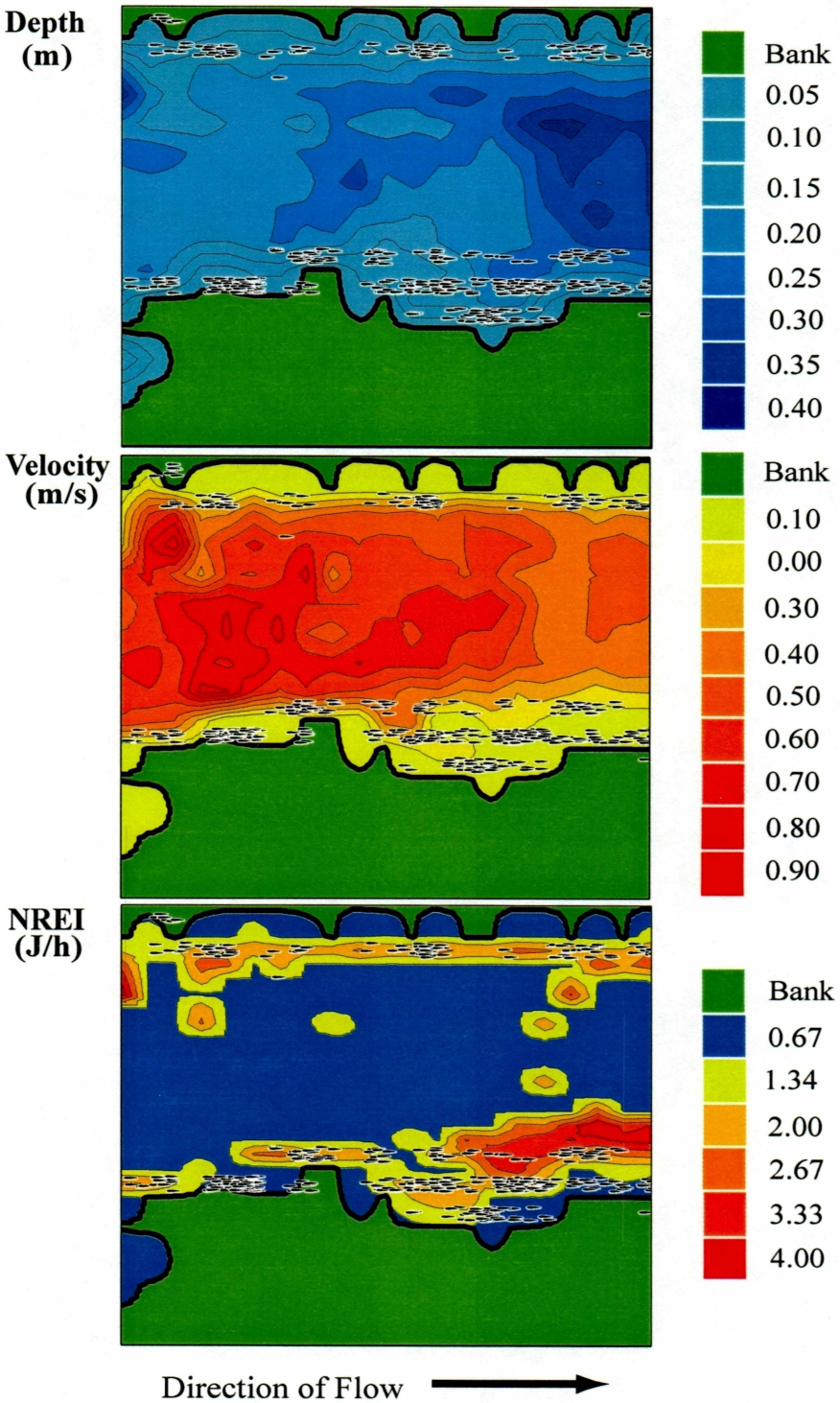

Figure 23.-Arctic grayling distribution maps showing depth, velocity and predicted net rate of energy intake (NREI) contours at Bona, June 2000.

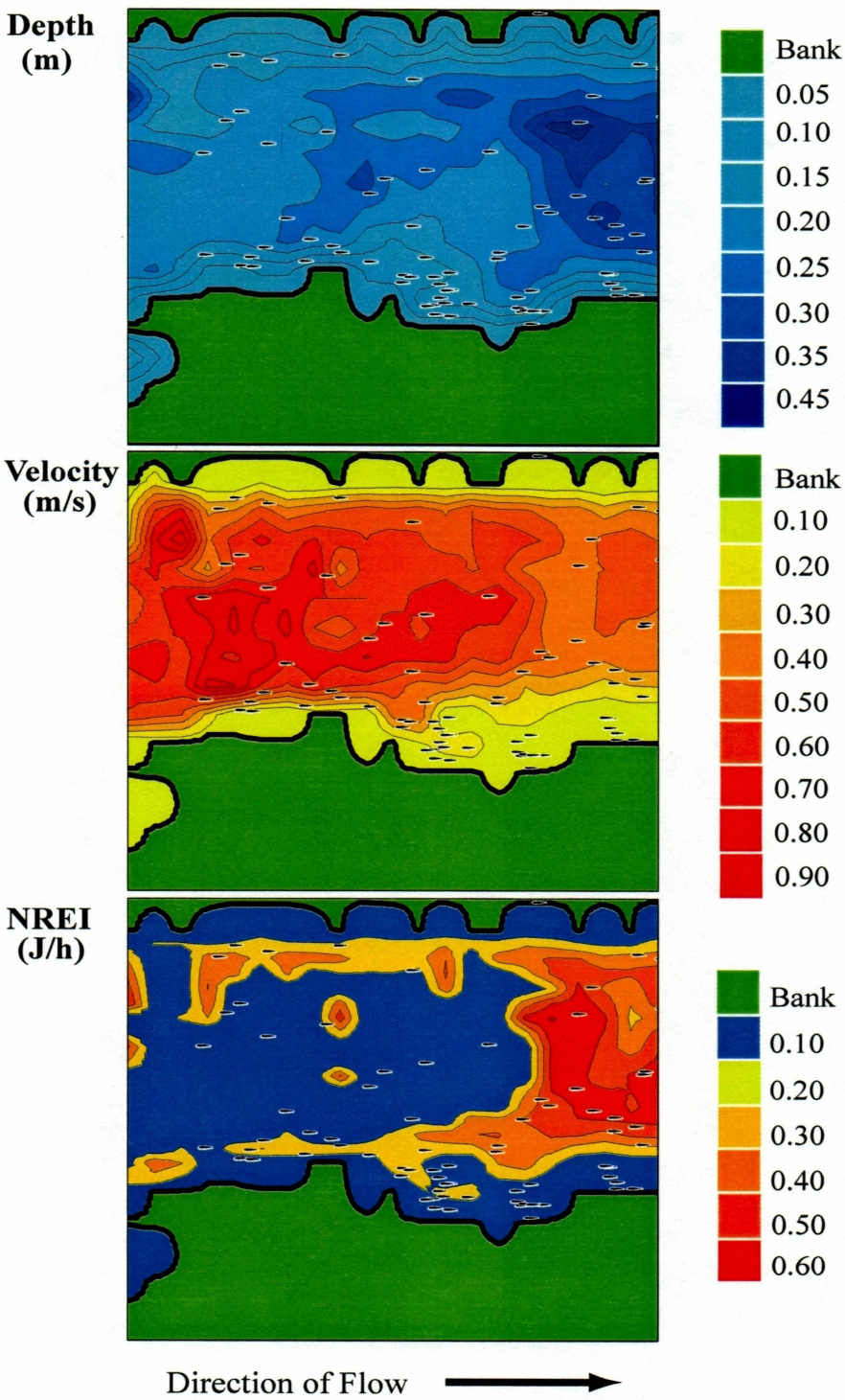

Figure 24.-Arctic grayling distribution maps showing depth, velocity and predicted net rate of energy intake (NREI) contours at Bona, July 2000.

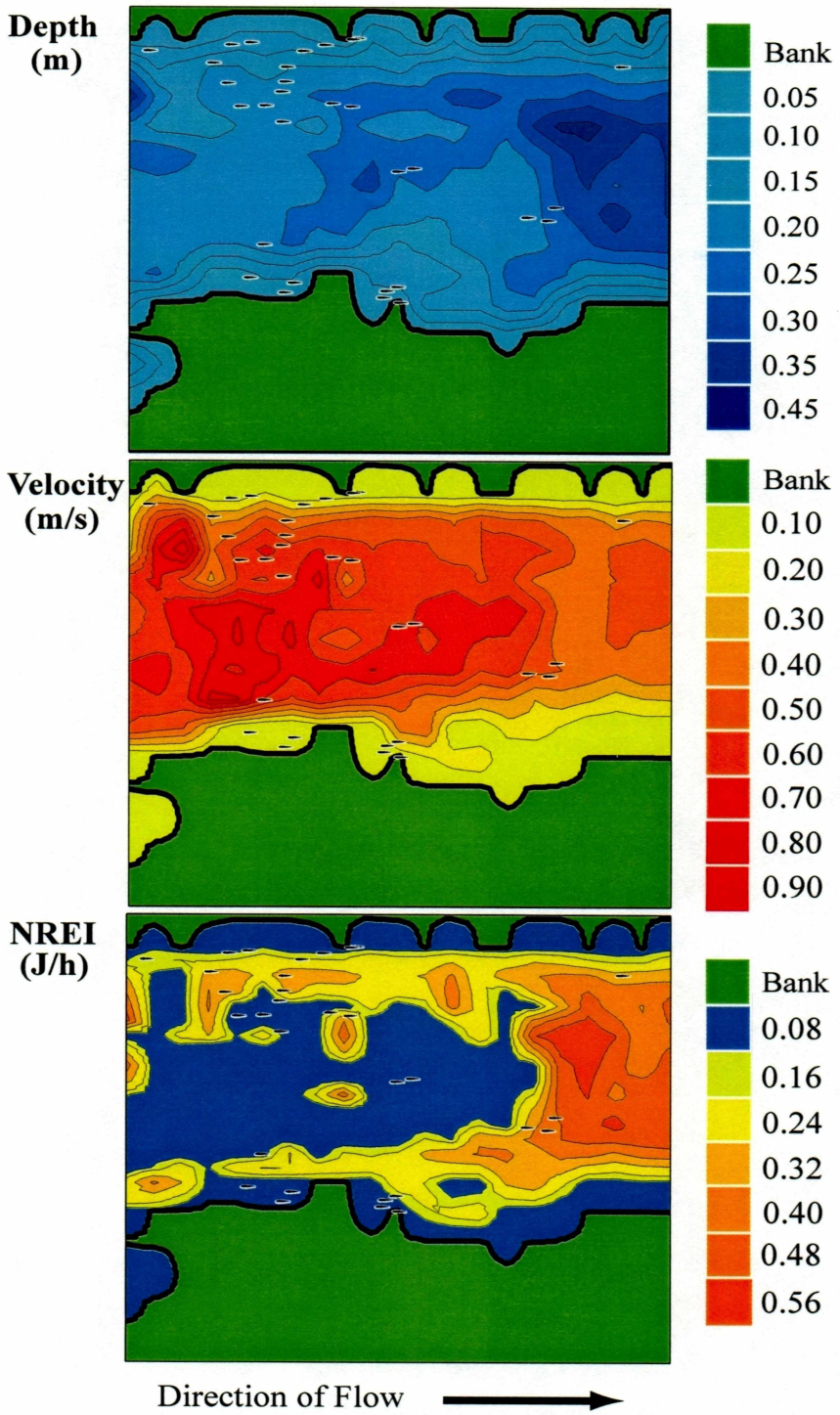

Figure 25.-Arctic grayling distribution maps showing depth, velocity and predicted net rate of energy intake (NREI) contours at Bona, August 2000.

observed throughout the entire reach, and on 16 August 31 fish averaging 62 mm were observed in moderately fast, deeper sections of the main channel.

The ratio of maximal NREI between reaches was similar to the ratio between the observed number of fish in each reach on all three dates, particularly in July and August (Table 4). The model predicted that fish abundance at Bona would be 2.7 times higher than Nordale in June, whereas the video survey showed they were 2.2 times as abundant. The model predicted that fish would be 0.09 and 0.07 times as abundant at Bona in July and August respectively; the video survey showed they were actually 0.08 times as abundant in both months.

Discussion

The model made accurate predictions of fish distribution in June and August; however, the model did not work well in July at either reach. As with other salmonid studies, Arctic grayling preferred habitats within stream reaches that were predicted to yield high energetic values (Fausch 1984; Hughes and Dill 1990; Nislow et al. 2000; Guensch et al.2001) and avoided areas with negative or very low energetic values.

Overall the model accurately predicted ontogenetic habitat shifts from June to August at both reaches. As with age-0 European grayling *Thymallus thymallus*, larval Arctic grayling occupied stream margins and backwaters (Scott 1985; Sempeski and Gaudin 1995) and moved to faster, deeper water as they grew (Scott 1985; Bardonnet et al. 1991).

Table 4.-Arctic grayling abundance, net rate of energy intake and the ratio of Arctic grayling abundance and net rate of energy intake at Nordale and Bona (B:N), 2000.

Month	Nordale	Bona	Ratio B:N
		Net rate of energy intake	
June	1.37	3.7	2.70
July	5.47	0.51	0.09
August	1.71	0.12	0.07
		Fish abundance	
June	206	441	2.14
July	954	76	0.08
August	372	31	0.08

Departures from the model's predictions in July and August at Bona and in June at Nordale were the result of fish occupying faster, shallower water than predicted by the model. This may be because fish preferred shallow water as it provided easier access to prey drifting on the water surface. It may also be because the model makes inaccurate assumptions about the way that water velocity influences feeding rate or an oversimplification in the way the model describes habitat. At Nordale fish densities were very high in July and it is likely that social interactions were forcing some fish to occupy less profitable habitats. When fish abundance was lower in August the model's predictions were more accurate.

The habitat selection model does not account for spatial variation in predation risk, and fish may be avoiding areas with profitable depth and velocity combinations because they are at a higher risk for predation. I have observed predation of age-0 Arctic grayling by northern pike *Esox lucius*, belted kingfisher *Ceryle alcyon*, slimy sculpin *Cottus cognatus* and round whitefish *Prosopium cylindraceum*. This is an important factor to consider because several studies have shown that fish will avoid areas of abundant food if they are susceptible to predation (Mittlebach 1981; Werner et al. 1983; Power 1984, 1987; Gilliam and Fraser 1987); thus, predators can influence decision-making processes that affect habitat selection and fish distribution. Fish may be immigrating into Nordale for cover (vegetation, woody debris, boulders) from predation and emigrating from Bona due to lack of cover. The stream margins at Bona offer some cover due to riparian vegetation, but there is no cover in the faster, deeper

sections of the channel. Incorporating predation risk is a goal for the future because currently no practically applicable model is available for stream fish.

The distribution of fish between the two reaches appears to be consistent with IFD theory. Arctic grayling distributed themselves such that the proportion of fish foraging in a reach equaled the proportion of resources available within that reach. Arctic grayling behaved as if they had knowledge of the differences in resource availability between reaches and were able to move freely between reaches (Power 1983; Grand 1997). The poor performance of IDF theory in June may be a result of the fact that the distribution of larval fish is strongly determined by the spawning habitat selected by their parents.

The reduction in fish density between June and July shows that Arctic grayling are either emigrating from Bona or experiencing high mortality as density declined more than 80% from June to July (441 to 76). This corresponded with a decline in NREI of more than 3-fold from 3.70 J/h to 0.12 J/h. Arctic grayling are immigrating into Nordale during the same period as density increased more than 75% from June to July (206 to 954). This corresponded with an increase in NREI of more than 5-fold from 1.37 J/h to 5.47 J/h.

The observable decline in fish density at Bona from June to July, and at Nordale from July to August, may be the result of self-thinning, a form of intraspecific competition found in food- or space-limited populations in which food or space requirements of an individual increases as it grows. Self-thinning has been observed in several studies of stream-dwelling salmonids (Elliott 1993; Bohlin et al. 1994;

Armstrong 1997; Dunham and Vinyard 1997; Norwall et al. 2000) and may be also occurring with Arctic grayling.

SUMMARY

1. The temperature-based growth model made accurate predictions at Nordale, demonstrating its ability to assess thermal habitat quality. The model was also able to identify a possible critical period at Bona where it is likely that competition for food caused density-dependent mortality or emigration. These results indicate that water temperature is an important factor controlling growth rates of Arctic grayling in Chena Slough, but that low food availability can limit growth in some reaches.

2. The foraging model consistently overestimated mean prey size, showing that it needs further work before it will be able to make accurate predictions of prey availability. The most likely reason for the model's inaccuracy is that the presence of abundant suspended detritus caused fish to narrow the size of their reaction volume in response to the increased information processing demands associated with discriminating prey from detritus. This narrowing of the reaction volume would weaken selectivity for large, highly visible prey, producing inaccurate model predictions. The model did correctly identify the fact that prey sizes were remarkably small at Bona, and that the prey sizes consumed by fish there remained very small through the summer, rather than increasing with fish body size; which is typical for drift-feeding fish.

3. The habitat selection model made accurate predictions in June but was less successful in July and August. This shows that the model could accurately relate water depth and velocity to habitat quality for very small fish, but was less capable for larger fish. These errors for larger fish may have been a result of the fact that the model did

not account for social interactions or the influence of predation risk on habitat selection. Adding the logic of Ideal Free Distribution Theory to the model resulted in accurate predictions of the relative abundance of fish between the two reaches. Fish distributed themselves so that the proportion of fish foraging in a reach equaled the proportion of resources available in that reach. Fluctuations in fish density suggest that Bona has good quality rearing habitat for post-emergent fish in June (marginal areas) and that Nordale has better quality rearing habitat for larger fish in July and August (mid-channel areas).

MANAGEMENT IMPLICATIONS

1. The results of this study show that the seasonal temperature regime plays an important role in determining the size of fish at the end of the first growing season. The relatively warm temperatures in Chena Slough result in large fish that probably have a better chance of surviving to maturity than the smaller fish reared in the cooler waters of the nearby Chena River. Habitat management efforts should pay particular attention to possible changes in the seasonal temperature regime, slightly warmer waters might be beneficial but cooler waters will probably result in slower growth.

2. There is strong evidence that food abundance is so low in some reaches of Chena Slough that competition may be limiting growth, causing density-dependent mortality or emigration. This is surprising given the fact that the Slough is eutrophied and highly productive (Wuttig 1997). If this hypothesis is true, then a large number of fish being produced by the Slough could be food-limited, especially larger fish in July

and August. Habitat management efforts should consider possible changes in the abundance, taxonomic composition, and size of drifting invertebrates.

3. The habitat selection model's accurate prediction of fish distribution in June showed the importance of marginal areas for post-emergent fish. This demonstrates the importance of maintaining habitat with the depth and flow characteristics of the natural stream banks. In particular woody debris and natural emergent vegetation are likely to provide higher quality habitat than non-vegetated stream banks. The models' successful prediction of the ontogenetic shift into faster water showed the importance of maintaining adequate water depths and velocities for larger fish in July and August. The habitat at Nordale appears to be particularly suitable for fish in July and August, perhaps due to details of depth, flow, and substrate that we do not yet understand. Habitat management efforts should consider possible changes to the nature of the banks, depth, flow, and substrate characteristics of the channel.

4. These findings suggest that high quality habitat for Arctic grayling in Chena Slough has the following characteristics: relatively high water temperatures that approach the growth optimum of 17 °C; naturally vegetated margins with emergent vegetation and woody debris; shallow water and slow flow; open channel areas with moderate depth and fast flow; a bed of gravel and vegetation; and high densities of small prey in June and moderate to high densities of larger prey in July and August.

RECOMMENDATIONS FOR FURTHER RESEARCH

This study has increased our knowledge about Arctic grayling habitat in Chena Slough, but it also demonstrates that there are several aspects we do not fully understand and require further research, particularly if we are to understand the affects of habitat change on Arctic grayling.

1. We need to understand the implications of changing discharge on the seasonal thermal regime. Discharge in Chena Slough is thought to have declined steadily over the years, and future restoration and enhancement efforts may augment existing flows.

2. We need to understand how changes in discharge would affect the depth and flow characteristics within the stream channel to determine if the net changes will be beneficial for Arctic grayling. Hydraulic modeling combined with fish habitat selection modeling (including ground-water and upwelling influences), could provide answers to this question.

3. We need to understand the ecological role of the extensive slow water areas in Chena Slough. These areas have been overlooked and we do not know the role they play in determining the productivity of the Slough.

4. We need to learn more about the invertebrate communities in Chena Slough to understand spatial variations in the abundance, size, and taxonomic composition of invertebrate drift. These variations are important in determining the productive capacity of different reaches within the Slough.

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